INNOVATIONS AND SOCIAL BARRIERS IN ORANGUTAN CULTURE

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von

Anna Marzec

aus

Polen

Promotionskommission

Prof. Dr. Carel P. van Schaik (Vorsitz der Dissertation)

Dr. Maria A. van Noordwijk (Leitung der Dissertation)

Prof. Dr. Barbara König

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Summary

Culture is defined as all of the knowledge and behaviors learned and transmitted through social learning between and within generations. As such, culture is present in many animal species. However, some aspects of human culture remain unique, namely its diversity and normativity. Above all, human culture is cumulative, and hence complex, as it constantly develops by building upon already acquired knowledge and by adding new innovations with incredible speed – technology is a clear example of this process. Non-human primates, as well as many other taxa, exhibit cultures that are much simpler than that of humans. Despite the differences, studying social learning of innovations and the resulting behavioral variation in our closest living relatives, the great apes, allows us to gain a better understanding of the evolution of human culture. The aim of this dissertation is to foster our understanding of the importance of cultural transmission in orangutans and to attempt to distinguish cultural units among orangutans. More specifically, I studied the mechanisms of knowledge and skill acquisition, the conditions favoring the occurrence of innovation, and the role of social barriers in social transmission of knowledge, skills and innovations.

Orangutans have slow life histories and are known to acquire all of their knowledge and skills socially prior to weaning. They are semi-solitary, with varying degrees of sociability among different populations. Females are philopatric and show a preference for associating with maternal female relatives while males disperse after reaching sexual maturity. It has been shown that orangutans have extensive cultural repertoires that are vertically and obliquely transmitted to immatures. Moreover, captive studies have shown that orangutans can be very innovative, extremely explorative and curious. Yet, none of these characteristics are observed in wild orangutans, who exhibit high level of neophobia and hardly ever explore. In fact, after reaching the age of first reproduction, the behaviors used as indirect measures of both social learning (i.e. close intent observation, so called "peering") and solitary learning (i.e. exploration) decrease dramatically and are in fact close to zero. This difference in behavior between wild and captive orangutans leads to the following questions: Under what conditions do orangutans innovate in the wild? And what are the factors limiting the spread of innovations? Since orangutan social organization suggest the existence of small social units within the population, we are interested in the effect of social barriers on the social transmission of knowledge, skills and innovations between these units. To address these questions, we studied both wild and ex-captive reintroduced orangutans.

This dissertation is divided into two parts. In the first part (Chapter 2), we focus on knowledge acquisition, and investigate whether necessity is one of the mechanisms driving innovativeness and exploration in orangutans. Interestingly, previous studies on wild populations living in habitats with fluctuating fruit productivity did not show that necessity (i.e. low availability of fruit) causes orangutans to explore new food sources and to innovate by adding new items to their diets. However, it is likely that in these studies the necessity threshold has not been exceeded since orangutans living in these habitats have already acquired full diet repertoire including the knowledge about available fallback foods. As such, there is no need for them to take unnecessary risks and try unknown food items that may be poisonous. Therefore, in order to really look at the role of necessity, we studied orangutans in an extreme condition – individuals reintroduced into a new habitat in which they did not grow up and thus lacked the local knowledge. We used a reintroduction program as a 'natural experiment,' which allowed us to investigate how orangutans acquire basic, but key, knowledge such as their diet. In addition, we compared the reintroduced individuals with a matched sample of individuals from another, wild population. We could show that reintroduced orangutans use a mix of solitary and social learning to acquire their diet. Moreover, we also showed that as their knowledge increased (i.e. time spent in the new habitat since reintroduction) the intensity of social and solitary learning decreases, suggesting that necessity is in fact the mother of invention in these orangutans in unusual conditions.

In the second part of this dissertation, I investigate the existence (Chapter 3) and role (Chapter 4) of social barriers in the spread of knowledge, skills and innovations in wild orangutan population. This question is interesting because orangutans do not have clearly defined social units with clear membership, and we can therefore expect different answers for different behaviors, depending on their salience or ease of transmission. The third chapter reports a unique observation of lethal aggression between two unrelated females, which show that under crowded conditions the relationships between matrilines can become extremely hostile, which would greatly hamper social transmission of skills and knowledge, despite high overlap in home range use. In order to investigate whether these social barriers have an effect on the transmission of knowledge and skills and thus lead to the existence of cultural units, we looked in the fourth chapter at nest construction elements and choices associated with the selection of nesting sites. The skills to build sleeping platforms are known to be learned socially and involve extensive practice. Thus, we investigated various nest related choices, behaviors and building techniques in order to see whether there are patterns in variation between resident

females and migrant males as well as between unrelated females. We found that orangutans have extremely large repertoires of nest building behaviors and techniques, and that they are extraordinarily flexible in combining them. Even though the majority of investigated choices and behaviors were universal within the population, some of them where concentrated within smaller units. Furthermore, we provide additional evidence for multiple tree nests being a cultural variant, and suggest that tree species choice might also be cultural since it varies between geographically separated populations that have access to the same tree species. In conclusion, we provide evidence for the existence of social barriers in a natural population of orangutans and we show that these social barriers may limit the spread of some innovations but not others.

In short, the results of these studies 1) show that necessity makes orangutans more innovative, 2) provide further evidence for the existence of social barriers, and 3) show that there is no fixed cultural unit in this species. In fact, the size of the cultural units differs depending on the behavior in question.

Moreover, the results presented in the second chapter have additional implications for orangutan conservation efforts. Since orangutans without role models run potentially lethal risks by independently exploring their new habitats, and social learning strongly facilitates the acquisition of vital skills, we suggest that reintroduction programs should preferably try to structure their releases so that naïve individuals can benefit from the experience of previously released individuals, who can serve as role models.

Ringkasan

Budaya didefinisikan sebagai semua pengetahuan dan perilaku yang dipelajari dan ditansmisikan melalui pembelajaran sosial di dalam dan antar generasi. Berdasarkan definisi tersebut, budaya dapat ditemukan dalam banyak jenis spesies hewan. Namun, beberapa aspek budaya manusia tetaplah unik, yaitu keanekaragaman dan norma-normanya. Di atas segalanya, budaya manusia bersifat kumulatif dan karenanya bersifat kompleks, karena terus-menerus berkembang dengan berfondasi pada pengetahuan yang sudah diperoleh melalui penambahan inovasi baru dengan kecepatan yang luar biasa, perkembangan teknologi adalah contoh jelas dari proses ini. Primata non-manusia, serta banyak taksa lainnya, menunjukkan budaya yang jauh lebih sederhana daripada yang ditemukan pada manusia. Meskipun terdapat perbedaan, mempelajari pembelajaran social dari inovasi dan variasi perilaku yang dihasilkan pada kera besar sebagai kerabat terdekat kita, memungkinkan kita untuk mendapatkan pemahaman yang lebih baik dari yang evolusi budaya manusia. Tujuan dari disertasi ini adalah untuk mendorong pemahaman kita tentang pentingnya transmisi budaya di orangutan dan untuk mencoba untuk membedakan unit budaya di orangutan. Lebih khusus lagi, saya mempelajari mekanisme akuisisi pengetahuan dan keterampilan, kondisi yang mendukung terjadinya inovasi, dan peran hambatan sosial dalam transmisi sosial pengetahuan, keterampilan dan inovasi.

Orangutan memiliki riwayat kehidupan yang lambat dan diketahui telah memperoleh semua pengetahuan dan keterampilan sosial sebelum waktu sapih. Mereka semi-soliter, dengan tingkat sosiabilitas yang bervariasi di antara populasi yang berbeda. Betina merupakan philopatric dan menunjukkan suatu preferensi untuk berasosiasi dengan kerabat betina sementara jantan menyebar keluar setelah mencapai dewasa kelamin. Telah ditunjukkan bahwa orangutan memiliki repertoar budaya yang luas yang ditransmisikan secara vertikal dan serong kepada individu yang belum dewasa. Selain itu, studi pada hewan captive menunjukkan bahwa orangutan bisa menjadi sangat inovatif, sangat exploratif dan memiliki rasa kaingin tahuan yang besar. Namun, tak satu pun dari karakteristik ini diamati pada orangutan liar, yang lebih menunjukkan tingkat neophobi yang tinggi dan hampir tidak pernah mengeksplorasi. Bahkan, setelah mencapai yang usia dari reproduksi pertama, perilaku yang digunakan sebagai ukuran tidak langsung dari kedua pembelajaran sosial (contohnya pengamatan dekat, disebut sebagai “peering”) dan pembelajaran soliter (contohnya eksplorasi) menurun secara dramatis dan bahkan mendekati nol. Perbedaan dalam perilaku antara orangutan liar dan orangutan dalam penangkaran mengarah ke berikut pertanyaan berikut: Dalam kondisi apa orangutan berinovasi di alam liar? Dan faktor apa yang menjadi faktor pembatas dalam penyebaran inovasi? Karena

organisasi sosial orangutan menunjukkan keberadaan unit sosial kecil dalam suatu populasi, kami tertarik pada efek hambatan sosial pada transmisi sosial pengetahuan, keterampilan, dan inovasi di antara unit-unit ini. Untuk menjawab pertanyaan ini, kita mempelajari baik orangutan liar maupun orangutan reintroduksi.

Disertasi ini dibagi menjadi dua bagian. Pada bagian pertama (bab 2), kami fokus pada perolehan pengetahuan dan menyelidiki apakah keharusan adalah salah satu mekanisme yang mendorong inovasi dan eksplorasi pada orangutan. Menariknya, penelitian sebelumnya pada populasi liar yang hidup di habitat dengan fluktuasi produktivitas buah tidak menunjukkan bahwa kebutuhan/keharusan (misalnya pada saat ketersediaan buah rendah) menyebabkan orangutan untuk mengeksplorasi sumber pakan baru dan berinovasi dengan menambahkan item baru sebagai pakan. Namun, ada kemungkinan bahwa dalam studi ini ambang keharusan belum terlampaui dikarenakan orangutan yang tinggal di habitat ini telah sudah memiliki repertoar pakan yanga lengkap, termasuk pengetahuan tentang menurunnya ketersediaan pakan pada waktu-waktu tertentu. Dengan demikian, tidak perlu bagi mereka untuk mengambil risiko yang tidak perlu dan mencoba pakan yang tidak diketahui yang mungkin beracun. Oleh karena itu, dalam rangka untuk benar-benar melihat peran dari “keharusan”, kami mempelajari orangutan yang dalam kondisi ekstrim: individu yang direintroduksi ke suatu habitat baru di mana mereka tidak tumbuh dan dengan demikian tidak memiliki satu pengetahuan lokal. Kami menggunakan program reintroduksi sebagai 'percobaan alami' yang memungkinkan kami mempelajari bagaimana orangutan memperoleh pengetahuan dasar tetapi utama seperti pengetahuan akan pakan mereka. Selain itu, kita membandingkan individu reintroduksi dengan individu lain yang serupa dari populasi liar. Kami bisa menunjukkan bahwa orangutan reintroduksi menggunakan campuran pembelajaran soliter dan sosial untuk memperoleh pakan mereka. Selain itu, kami juga menunjukkan bahwa selagi pengetahuan mereka meningkat (contohnya waktu yang dihabiskan di habitat baru sejak itu reintroduksi) intensitas pembelajaran sosial dan soliter menurun, menunjukkan kebutuhan merupakan bu dari penemuan pada orangutan dalam dalam kondisi yang tidak biasa ini.

Pada bagian kedua dari disertasi ini, saya menyelidiki keberadaan (bab 3) dan peran (bab 4) dari penghalang sosial di dalam penyebaran pengetahuan, keterampilan, dan inovasi dalam populasi orangutan liar. Pertanyaan ini sangat menarik karena orangutan tidak memiliki unit sosial yang jelas dengan keanggotaan yang jelas, oleh karena itu, kita bias mengharapkan jawaban yang berbeda untuk perilaku yang berbeda, tergantung pada arti-penting atau kemudahan transmisinya. Bab yang ke-tiga melaporkan pengamatan yang unik dari agresi

mematikan antara dua betina yang tidak terkait, yang menunjukkan bahwa dalam kondisi yang ramai hubungan antara matrilinear bisa menjadi sangat bermusuhan, yang akan sangat menghambat transmisi sosial keterampilan dan pengetahuan, meskipun orangutan memiliki tumpang tindih yang tinggi dalam area jelajah. Dalam rangka untuk menyelidiki apakah ini penghalang sosial memiliki efek pada para transmisi pengetahuan dan keterampilan dan menyebabkan terciptanya keberadaan unit budaya, kami melihat dalam bab keempat yang membahas elemen konstruksi sarang dan pemilihan lokasi bersarang. Keterampilan untuk membangun sarang tidur diketahui dipelajari secara sosial dan melibatkan latihan terus-menerus. Dengan demikian, kami menyelidiki berbagai pilihan, perilaku, dan yang terkait teknik membangun sarang untuk melihat apakah ada pola variasi antara betina penghuni area jelajah dan jantan migran serta diantara betina yang tidak terkait. Kami menemukan bahwa orangutan memiliki repertoar yang sangat besar dari perilaku dan teknik membangun sarang dan mereka sangat fleksibel dalam menggabungkan keterampilan ini. Meskipun mayoritas pilihan perilaku bersifat universal yang dalam populasi, beberapa perilaku terkonsentrasi dalam unit yang lebih kecil. Selanjutnya lebih, kami memberikan bukti tambahan untuk beberapa sarang pohon menjadi sebuah varian budaya dan menyarankan bahwa pilihan spesies pohon juga mungkin bersifat budaya karena bervariasi antara populasi yang terpisah secara geografis yang memiliki akses ke spesies pohon yang sama. Kesimpulannya, kami memberikan bukti keberadaan hambatan sosial dalam suatu populasi alami orangutan dan kami menunjukkan bahwa hambatan sosial dapat membatasi penyebaran beberapa inovasi tetapi tidak untuk hal yang lain.

Singkatnya, hasil dari penelitian ini 1) menunjukkan bahwa kebutuhan membuat orangutan menjadi lebih inovatif, 2) memberikan bukti lebih lanjut akan keberadaan hambatan sosial, dan 3) menunjukkan bahwa tidak terdapat satuan budaya yang tetap di spesies ini. Bahkan, ukuran unit budaya berbeda tergantung pada yang perilaku yang bersangkutan.

Selain itu, hasil yang disajikan dalam bab kedua memiliki tambahan implikasi untuk upaya konservasi orangutan. Karena orangutan tanpa panutan memiliki risiko yang berpotensi mematikan karena mengeksplorasi secara mandiri habitat baru mereka, dan pembelajaran sosial sangat memfasilitasi perolehan keterampilan vital, kami menyarankan agar program reintroduksi sebaiknya mencoba menyusun pelepasan mereka sehingga individu yang naif dapat mengambil manfaat dari pengalaman individu yang dilepaskan sebelumnya, yang dapat berperan sebagai panutan.

Chapter 1: General introduction and summary of findings

Background

Human and animal culture

For a long time, culture was thought to be a uniquely human trait. However, an increasing number of studies has shown the presence of cultural variation in many animal species, and as such provided evidence that human culture is at the extreme end of a phylogenetic continuum (Whiten 2012). Thus, rather than its existence, it is the expression in humans that is different. First, human culture is far more diverse in that it encompasses many forms of technological knowledge, beliefs, arts and morals, to name just a few (Owen 1857, Tylor 1871). Second, human culture is undeniably more complex than cultures in the animal kingdom; and third, we are also the only species whose culture is normative (Whiten and van Schaik 2007, Laland and Galef 2009, Whiten 2017). Moreover, as humans we fully rely on culture simply because we acquire virtually all information, skills and knowledge through social learning, which generates cultural processes (Braidwood 1975).

In fact, the most liberal way to define culture in humans, and thus also in animals, is to consider as cultural 'all behaviors and knowledge that are acquired and passed on within and between generations through social learning' (Boyd and Richerson 1985). Even though some researchers indeed use this definition to study and describe animal culture (Fragaszy and Perry 2003, van Schaik 2010, Whiten 2017, Schuppli and van Schaik 2019) it is not the commonly accepted approach. In fact, there are numerous suggestions about what conditions (in addition to being a product of social learning) must be met for a behavior to be considered cultural: the behavior should be normative (McGrew 2004, Hill 2009), cumulative (Tomasello et al. 1993, Levinson 2006, Hill 2009), transmitted by imitation and/or teaching (Galef 1992), or transmitted across generations (Whiten and van Schaik 2007, Perry 2009a, 2009b). Here, given my focus on nonhuman apes, I remain on the liberal side.

It is very difficult to demonstrate the cultural process i.e. actual social transmission in nature, whereas it is much easier to observe its products i.e. patterns of variation in behavior. Thus, the geographic method was adopted to document the presence of culture in wild animals. Under this approach, in order to decide that a particular behavior or its variant is a result of social transmission and thus cultural, two other explanations have to be excluded (McGrew and Tutin 1978, McGrew 1992): (1) ecological differences between the populations to which

individuals may independently respond differently, and (2) population differences in genetic predispositions. The geographic method, also known as the ethnographic method or the method of exclusion (Whiten et al. 1999) classifies behavior as cultural when it has a customary or habitual presence in one but is absent in at least one other population, and this pattern cannot be explained by ecological or genetic differences (Galef, 1976, Nishida, 1987). The first reports of culture based on geographic variation in behavior come from long-term studies on chimpanzees (McGrew and Tutin 1978, Goodall 1986, McGrew 1992), with especially the exhaustive, multi-site comparison presented by Whiten et al. (1999) convincing many that great apes have cultural variation.

The etnographic method soon became the most commonly used tool to detect the presence of animal culture. It was used to demonstrate cultural variation in orangutans (van Schaik et al. 2003), bonobos (Hohmann and Fruth 2003), and gorillas (Robbins et al. 2016) as well as other primates (capuchin monkeys: Perry et al. 2003, Perry 2011; spider monkeys: Santorelli et al. 2011a, 2011b) and non-primate species (dolphins: Krützen et al. 2005, Kopps and Sherwin 2012; whales: Allen et al. 2013). These studies, despite not showing evidence for social learning, have amply documented the geographic inter-population variation in behaviors. Due to the nature of the method, most, if not all of the behaviors detected using this method are in fact innovations.

Innovations i.e. novel behavioral variants (e.g. tool use to extract food) may spread within the population, which may subsequently lead to inter-population variation (Kummer and Goodall 1985, Galef 1992, Galef and Allen 1995, Whiten 2000, Laland and Hoppit 2003). Since true innovations that persist in the population are generally rather rare (McGrew 2004), their distribution is likely to show geographic variation in the wild, and thus also help to recognize it as cultural (Galef 1976, Nishida 1987). Animal culture is therefore often defined as socially transmitted innovation (Imanishi 1957). The spread of innovation is possible in species with adequate social tolerance and social opportunities i.e. peaceful and/or friendly associations with conspecifics that allow close proximity between individuals and as such present opportunities to learn from each other (Coussi-Korbel and Fragaszy 1995, van Schaik et al. 1999). In addition, effective transmission of novel behavioral variants depends on the ability to produce innovations that are salient and thus likely to become prevalent (Pradhan et al. 2012a, van Schaik 2016). However, since the most commonly used method to detect culture in animals focuses on innovations that cannot be explained by ecological factors, it is likely to underestimate the size of cultural repertoires of the species given the likely presence of a

substantial number of behaviors that are socially learned adaptations to ecological conditions (Laland and Janik 2006, Gruber et al. 2009, Koops et al. 2013, 2014). Thus, some argue that the extent of culture we are describing using this method for many animal species, in particular the great apes, is in fact the 'tip of the iceberg' (Schuppli and van Schaik 2019).

Social learning

Social learning allows the acquisition of information or behavior patterns by observing, associating with, or interacting with another individual or the product of that individual's behavior (Heyes 2012). Social learning is widespread in the animal kingdom (Galef and Laland 2005, van Schaik et al. 2017) and it has been shown in many species, mostly in captive settings (Galef and Laland 2005, Rapaport and Brown 2008, Reader and Biro 2010, Whiten 2017, Whiten and van de Waal 2018), but also in the wild (Jaeggi et al. 2010, Perry 2011, van de Waal et al. 2013, Hobaiter et al. 2014, Schuppli et al. 2016a, 2016b). Social learning is known to be a more efficient and less dangerous way to acquire necessary knowledge compared to individual learning. However, learning from others can be costly as it may potentially lead to acquiring non-adaptive behavior (Richerson and Boyd 2005, van Schaik 2010**)**. Nonetheless, on average, the benefits of social learning exceed its costs, for instance, because it reduces the risks associated with individual exploration and trial-and-error learning, such as accidentally consuming poisonous food items (Galef and Giraldeau 2001). Moreover, social learning allows an individual to benefit from the knowledge of more experienced role models and thus increases the likelihood of learning relevant information much faster compared to independent learning (Laland 2004). As a result, social learning significantly increases the repertoire of learned skills and plays an important role in skill acquisition (Tomasello 1999, van Schaik and Burkart 2011, van Schaik et al. 2017) by stimulating individual practice following the observation (i.e. the peering-practice cycle, see Schuppli et al. 2016a).

Social transmission can occur between or within generations. In the first case information is learned either from the parent, i.e. vertical learning (Boyd and Richardson 1985), or from another adult group member, i.e. oblique learning (van Schaik 2010, van Schaik 2016). In the second case, information is spread among peers, i.e. horizontal learning (Laland et al. 1996). Only the behavioral variants that persist in the population over multiple generations are usually considered cultural, and vertical or oblique social learning is therefore considered an essential element of culture.

There are numerous mechanisms of social transmission of information (see Whiten and Ham 1992, Heyes 1994). One of the simplest forms of social learning is local or stimulus enhancement. For example, in many instances diet acquisition can be explained by enhancement, when associating with experienced conspecifics during foraging is enough to learn where to feed and what to feed on (Rapaport and Brown 2008). For example, pigeons locate a feeding site faster when conspecifics are already feeding there (Palameta and Lefebvre 1985). A form of stimulus enhancement, observational conditioning, allows the individual to learn to develop fear responses toward a specific stimulus (Mineka and Cook 1988). However, local or stimulus enhancement and observational conditioning are seen by some as distinct processes while other researchers treat them as the opposite (positive and negative) versions of similar process (Whiten and Ham 1992, Heyes 1994). A more effective, cognitively complex and in fact most sophisticated mechanism of social learning is imitation i.e. copying the action of others (but see Horner and Whiten 2005). Since imitation is a very important form of learning in human children (McGuigan and Graham 2010) as well as adults (Whiten et al. 2009) and thought by some to be crucial requirement for culture (Galef 1992) the evidence of copying skills in apes is of great relevance. Experiments have shown that both chimpanzees (Whiten et al. 1996, Whiten 1998, Horner and Whiten 2005, Hopper et al. 2008) and orangutans (Russon and Galdikas 1993, Bering et al. 2000, Stoinsky and Whiten 2003) are able to copy actions performed by a model, to reach a specific goal (but see Tennie et al. 2009). Nonetheless, the experiments have their limitation. Not only their duration is shorter than normal social learning processes in nature but it is also difficult to demonstrate which exact mechanisms of social learning are at work (Galef and Heyes 2004, van de Waal et al. 2013). Moreover, most relevant for the studies in the wild is the fact that knowledge and skills are indeed acquired socially rather than which particular mechanism of social learning is used. In fact, many species including humans, use a number of social learning mechanisms to acquire skills and knowledge. Thus, imitation is one of many mechanisms that under natural conditions allows transmission of behavioral details among individuals of the population in some animal species.

The fact that social learning is critical for acquisition of knowledge and skills has been shown in captive settings. When immatures apes are socially deprived and have no opportunity to learn from experianced role models they are generally unable to, for instance, build proper nests (Bernstein 1962, Videan, 2006) which is a universal skill showed by all wild apes. Even though in orangutans the basic nest structure appears to be comparable across populations, and as such it is likely a latent solution to the problem (Tennie et al. 2009), it still takes wild young

orangutans years of close observation and practice before they are able to build well-functioning, stable nests themselves (Schuppli et al. 2016a). The same is true for other skills and knowledge, and is especially important for these that are necessary for survival, for instance assembling the diet. This is why conservation measures such as reintroduction or translocation (i.e. moving of an individual to a new habitat in which it did not grow up; IUCN 2013) carry a high risk of failure due to individuals' lack of appropriate knowledge, in particular in species like great apes that strongly rely on knowledge acquired socially.

Social learning has been demonstrated for a number of animal species (cephalopods: Fiorito and Scotto 1992; fish: Brown and Laland 2003; reptiles: Wilkinson et al. 2010; birds: Lefebvre and Bouchard 2003, Zentall 2004; and mammals: Boran and Heimlich 1999, Range et al. 2007), with great apes being, apart from humans, the most prominent 'social learners' (Tomasello 1996, Tomasello and Call 1997, Custance et al. 2002, Heyes 2012). Therefore, if we apply the criteria used for humans (i.e. that all socially learned behaviors are cultural) to other species, in particular to our closest living relatives, who just like us learn most of their behaviors socially (Schuppli and van Schaik 2019, Whiten 2019), we will have to admit that they are nearly as cultural as humans are. Moreover, since not all culture is geographically variable, a lot of it presumably remains undetected (Schuppli and van Schaik 2019).

Innovation and barriers to their social transmission

Culture is generally inferred when behavior is geographically variable. However, geographic variation in behavior among different populations of the same species is not automatically considered to be cultural, even though that is the case in humans. One must show that this vairation is not linked to habitat or genetic differences, which could explain the variation by parallel and thus independent acquisition by the animals involved. Nonetheless, even if this can be done, we should still not expect the boundaries to coincide for each particular behavior.

Undeniably, physical barriers play a key role in social transmission. Comparison of different orangutan populations living in similar habitats but not exchanging migrants due to geographic separation, e.g. an impassable river barrier, revealed different traditions in diet but also other cultural variants (Bastian et al. 2010, 2012), as well as in the presence of tool use to extract *Neesia* seeds (van Schaik et al. 1996, van Schaik and Knott 2001). Genetic differences, though present, were very modest in this case, and in general did not explain much of the

geographic variation in orangutan behavioral ecology (Krützen et al. 2011). In fact, a similar effect has been seen in the presence of nut cracking behavior in different, geographically separated, populations of chimpanzees (Boesch et al. 1994, McGrew et al. 1997). Thus, the presence of dispersal barriers is the most likely cause of cultural boundaries, and may set the 'grain' of cultural variation in a species.

However, it is likely that not only geographic barriers limit the spread of innovations. Social barriers may also play a role. They depend on social organization, and therefore may vary by species. In addition, they may differ for different types of behavior, whose spread may depend on e.g variation in salience, proximity required to infer the behavior, or sex of the observer and demonstrator (immigrant or resident).

Social barriers and social integration may contribute to variation in behavioral patterns within a genetically homogeneous population. It has been shown that social barriers do influence the transmission of parasites. In group-living primates, parasite transmission shows a positive association with increased social exposure (MacIntosh et al. 2012). A similar effect is expected for transfer of knowledge and novel behaviors or their variants, such as lobtail feeding in whales (Allen et al. 2013) or sponging water using moss by wild chimpanzees (Hobaiter et al. 2014). In fact, when opportunities for horizontal transmission are limited, some of the behaviors may either disappear or become very rare and restricted to small social units such as matrilines (van Schaik and Knott 2001). Thus, social barriers may potentially have a similar effect to the geographic ones with the difference that they will act at a smaller scale by affecting the cultural variation within populations.

Another potential social barrier might be present due to conformity. It is possible that if a group imposes a particular behavior onto their new group members, a novel behavioral variant introduced by new immigrants may not spread. Studies showed that group-specific behaviors such as selection of hammers for nut cracking is highly uniform in chimpanzee communities and that the group's behavior is actively adopted by new members even if their originally expressed behavior was different (Luncz and Boesch 2014). Similar results were found in vervet monkeys, where males who immigrated switched their food preference to that of their new group (van de Waal et al. 2013).

Finally, within-population social differentiation might arise due to individual bias in social interest as well as opportunities to associate with preferred role models, which depends on gregariousness and social organization of the species. It has been shown that immature orangutans pay more attention to rare behaviors, which are less familiar or unfamiliar to them,

when performed by a trusted role model (mother) rather than someone else. However, already during early development sex differences in skill acquisition are observed, e.g. in diet, with young females developing broader diets faster than males do (Schuppli et al. 2016b). Similarly, immature chimpanzee females learn termite-fishing behavior faster and outperform male peers (Lonsdorf 2005).

Aim of this dissertation

The first aim of this dissertation is to investigate the importance of social learnig in skill acquisition and the conditions necessary for innovations in reintroduced Bornean orangutans (chapter 2). The second aim is to provide evidence for the existence of social barriers as well as investigate the potential effects of social barriers on within-population cultural variation in wild Bornean orangutans (chapters 3 and 4).

In fact, orangutans are an ideal species to study innovations, social learning and barriers in social transmission. They have rich cultural repertoirs yet rarely innovate (van Schaik et al. 2016). They show high levels of exploration, innovation and curiosity in captive conditions while being extremly neophobic and conservative in the wild (Forss et al. 2015, Damerius et al. 2017). Thus looking at an extreme situation, in which mature individuals are reintroduced in habitat that is unknown to them and in which they therfore need to acquire necessary skills may shed light onto how orangutans acquire their knowledge under such unusual conditions. Reintroduction of orangutans is thus a 'natural experiment' that allows us to investigate how important social learning is for them as well as whether necessity makes them more exploratory and innovative. Moreover, since wild orangutans aquire all their skills socially but their social organization lacks distinct social groups and the number of opportunities for social learning outside mother-offspring dyads is limited, they are ideal candidate to investigate the existence and possible effects of social barriers. These barriers may produce cultural variation within populations,

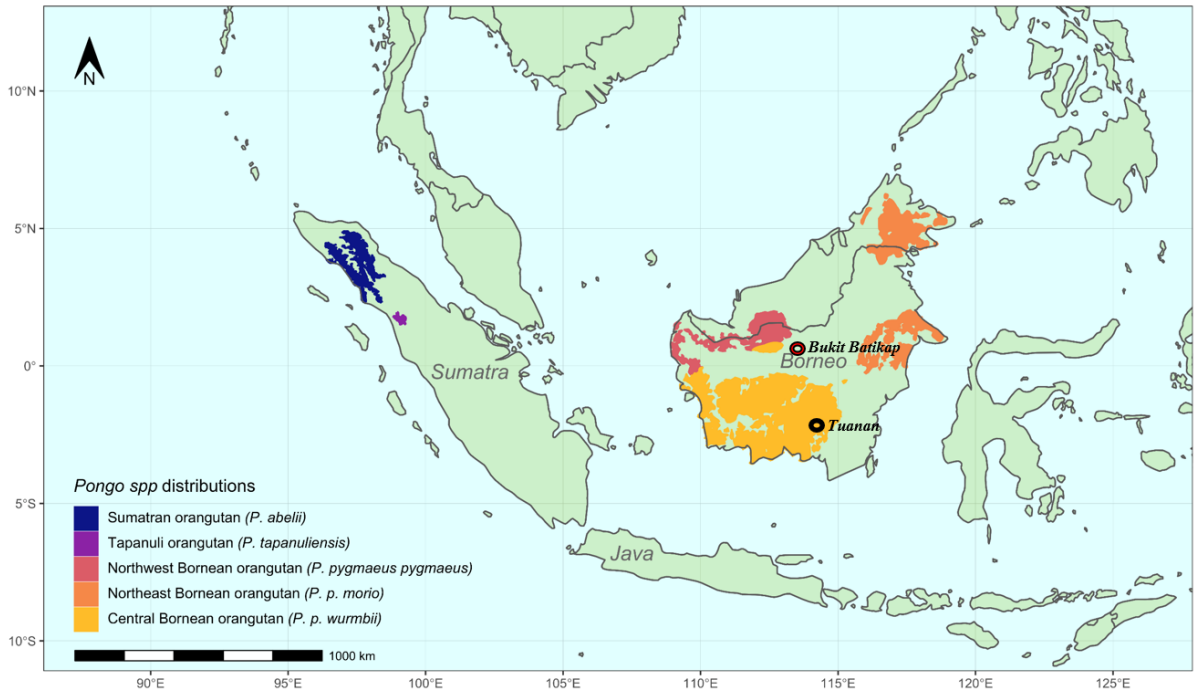
Study species and study sites

Orangutans

Orangutans (*Pongo spp*.) inhabit the islands of Borneo (one species *Pongo pygmaeus* with three subspecies: *P. p. pygmaeus pygmaeus, P. p. wurbii, P. p. morio*) and Sumatra (two

species: *P. abelii* and *P. tapanuliensis*) (see fig 1 for the distribution). All three species are critically endangered (IUCN 2019). Orangutans are large-brained and show great flexibility in social system, ranging from semi-solitary to low-level fission-fusion across different populations (van Schaik 1999, Mitra Setia et al. 2009, van Schaik et al. 2009).

Fig.1. Distribution of orangutan species and subspecies with marked location of study sites: wild population of *P. p. wurmbii* at Tuanan in Central Kalimantan, and reintroduced population at Bukit Batikap, Central Kalimantan. (*Pongo spp* distributions sources: IUCN Red List of Threatened Species (*P. abelii* – Singleton et al. 2017; *P. tapanuliensis* – Nowak et al. 2017; *P. pygmaeus* – Ancrenaz et al. 2016; map made by A. Ashbury)



Social organization in orangutans

In orangutans, females are the philopatric sex and stay in the area where they were born. Upon reaching maturity, females establish their home ranges, often overlapping with those of other females, including their mothers and sisters. Nonetheless, home range overlap between unrelated female dyads is also appreciable in habitats with a high density (Wartmann et al. 2010). In addition, regardless of the degree of home range overlap, females show a preference for associating with related rather than unrelated females. Thus, females form matrilineal clusters, both spatially and socially (Arora et al. 2012, van Noordwijk et al. 2012, Ashbury et al. subm.). Moreover, the existence of antagonism and thus real social barriers within the orangutan population is supported by recent observation of lethal aggression between non-

related females (Marzec et al. 2016 – chapter 2) as well as an increase in aggression among them in times of food scarcity (Meric de Bellefon 2017). Males are the dispersing sex, but little is still known about the distance they travel after leaving the natal area and the size of their range at different phases of their life.

Skill acquisition in orangutans

Even more than other great apes, orangutans are known for their extremely slow life history. They have the longest birth intervals of all terrestrial mammals and are late at both weaning and first reproduction. Mothers form close, long lasting associations with their as yet unweaned offspring for 6-8 years before they give birth to a next one (van Noordwijk et al. 2018). These close mother-offspring bonds allow immatures repeated close-distance observation of their mother's activity (peering) over many years. Orangutans acquire their behavioral repertoire, including what to eat and how to process food, cross gaps in the canopy, and make nests, socially by peering followed by independent practice (the so-called peer-practice cycle). As such, by the time they are weaned at the age of 6-7 years, immatures have the same diet repertoire as their mothers (Jaeggi et al. 2010, Schuppli et al. 2016b). Young orangutans learn all the necessary skills needed for survival from their mothers and later in life acquire some additional behavioral variants or innovations mostly through social learning from peers.

Recent studies have shown a sex bias in social interest towards different role models and behaviors in older, independent and mature orangutans (Mörchen 2016, Wassmer 2019, Ehmann et al. MS). It has been suggested that sex-biased dispersal may explain why male orangutans may continue to learn later into adulthood than females (Wassmer 2019). Under natural conditions males need to acquire new knowledge about the area they disperse into, while females remain all their life in the same place they grew up in (Ashbury et al. subm.). However, these sex differences likely do not reflect the actual abilities of learning at adult age in this species, but rather the necessity of it (see chapter 4).

Culture in orangutans

Under natural conditions, mature orangutans seem to rely fully on their socially acquired knowledge. Orangutans' abilities for social learning have been shown in captivity (Russon and Galdikas, 1993, 1995) and, more indirectly, in the wild (Jaeggi et al. 2010, Bastian et al. 2012,

Schuppli et al. 2016a). However, given the orangutans' solitary lifestyle and female preference for associating with female relatives, the opportunities for social learning are limited for adult individuals. Nonetheless, important innovations (e.g. way of extracting valuable food), even though rare, once made are likely to spread and be retained in the population thanks to mostly vertical and oblique social transmission. As a result, orangutans have rich behavioral repertoires (van Schaik et al. 2016).

Comparisons from multiple long-term studies showed extensive geographic variation in behavioral ecology, social organization as well as putative culture of orangutans (van Schaik et al. 2009, Wich et al. 2009). Research shows that variation in behavior between orangutan populations living in similar habitats, but separated by a physical barrier, thus without exchanging migrants, are best explained by local adaptation through developmental plasticity (Bastian et al. 2010). Two components of behavioral plasticity, namely individual learning and social learning of local innovations (i.e. tool use, foraging techniques, comfort or social behaviors), play a key role in explaining the geographic variation (Krützen et al. 2011, Bastian et al. 2012). The question remains whether social barriers could have a similar effect and lead to behavioral variation within populations (chapter 3).

Moreover, individual exploration by mature individuals is extremely rare and as a result innovations are too. Since wild orangutans are very novelty-averse (Forss et al. 2015) and show little exploratory tendencies in natural conditions it is puzzling under what conditions they do innovate. We address this question in chapter 4.

Study sites

This study was conducted in two locations: Tuanan and Bukit Batikap both situated in Cantral Kalimantan, Indonesia (see fig. 1).

Tuanan Orangutan Research Project is a long term collaboration directed by Dr. Maria van Noordwijk (University of Zurich), Dr. Suci Sri Utami Atmoko (Universitas Nasional in Jakarta) and Dr. Erin Vogel (Rutgers University). Study site is located within Mawas Conservation Area managed by Borneo Orangutan Survival (BOS) Foundation. The wild orangutan population has been intensively and continuously studied since 2003. Long-term behavioral and spatial data are available and were used in addition to data I have collected during my fieldwork.

Bukit Batikap is an orangutan reintroduction project initiated and carried out by Borneo Oorangutan Survival (BOS) Foundation. Ex-captive, rehabilitated orangutans are released into the suitable habitat, which is within the species' historical range. Orangutans are monitored post-release in order to assess the success of the reintroduction process. Even though released individuals are not normally provided with supplementary food, in some cases (e.g. illness, injuries or obvious failure to adapt to new habitat) human intervention is provided. This artificially created orangutan population provides an experimental setup and unique opportunity to study skill acquisition in mature orangutans moved into a novel habitat.

Detailed description of both sites as well as data collected and methods used are provided in each chapter.

Content of this dissertation and summary of findings

This dissertation has two parts. In the first part containing one chapter (chapter 2) I examine skill acquisition among mature individuals and the role of necessity in innovation in orangutans that were introduced to a novel environment unfamiliar to them. The second part contains two chapters. In chapter 3, I present evidence supporting the existence of social barriers in this species, and in chapter 4 I investigate potential effects of social barriers on cultural variation within a population of wild Bornean orangutans.

Chapter 2: When is necessity the mother of invention? – Testing innovation in reintroduced Bornean orangutans (*Pongo pygmaeus*)

The aim of this chapter was to investigate under what conditions orangutans innovate and whether necessity is a mechanism at work. We used a natural experiment of the BOS reintroduction program to evaluate how mature, ex-captive orangutans acquire key knowledge such as diet in their new habitat. Reintroduced individuals have limited forest knowledge that varies between them depending on how much time they spent in natural habitat before being captured and moved to rehabilitation centers. Regardless of the level of forest skills acquired prior to reintroduction, they still have to learn everything in the habitat where they are released, which is partially or wholly new to them. What to eat and where to find food are key forms of knowledge for individual survival.

We investigated how naïve individuals acquire the necessary knowledge. We found that mature reintroduced orangutan females use a mix of independent exploration and social information to acquire the diet in their unknown habitat. The differences between newly reintroduced and experienced individuals in exploration and peering rates, as well as diet repertoire size showed that necessity indeed makes orangutans more exploratory and innovative. Moreover, using a comparative approach, we find the predicted differences in individual and social learning between wild and reintroduced mature orangutans.

In addition to providing further insights into skill acquisition in orangutans and showing the role of necessity in innovation in orangutans, this study also has implications for orangutan conservation. Our results show that orangutans who are newly reintroduced into foreign habitat attempt to seek social information from more knowledgable role models. Thus, these findings can be used for evaluation and modification of current reintroduction procedures.

Chapter 3: The dark side of the red ape: Male-mediated lethal female competition in Bornean orangutans

In this chapter we describe an unusual event, the first case of lethal aggression observed in orangutans. The attack, which involved two mature and unrelated females supported by males, shows the extent to which unrelated females may compete over resources, in particular in habitats with high density and increased pressure from the other resident females. Orangutans are critically endangered and overall numbers of each species are rapidly declining mostly due to habitat loss (Wich et al. 2008). However, in some locations (e.g. long-term research sites) increases in individual densities are observed due to protected status of both the species and the area. As the forest habitat is continuously shrinking the populations are squeezed into the remaining space, resulting in saturation of the available habitat. As a consequence, as more individuals are crowded into a limited space, competition for resources among females is exacerbated, and finds expression in higher level of intolerance towards conspecifics, especially non-kin. Even though in chimpanzees the rates of lethal aggression were not related to measures of human impacts (Wilson et al. 2014), the example of the violent aggression between unrelated orangutan females could be an indication of how intense the competition may become in a saturated habitat. This observation suggests that establishing a home range in already occupied space leads to an increase in aggressive encounters, especially between non-related females. It also supports the existence of social barriers between clusters of related females which in turn are likely to be a limiting factor for social transmission of innovations. In addition, the male

support in this unique aggression shows the extent of services males may provide to females. Although this was a first-ever such observation in orangutans in many years of research it may not be incidental and with increasing densities we may see more of such, so far unique, behaviors. In fact, in recent years we do observe increase in aggressive encounters between unrelated females as well as less time spent in association (active avoidance) of relatives (unpublished data), making the social barriers even more pronounced. Further studies are needed to investigate this prediction.

The main consequence of the presence of social barriers between female matrilines might be a more patchy distribution of cultural variants. This effect may become even more pronounced with increasing density of orangutans in a limited space unless males continue to connect these different matrilines.

Chapter 4: Within-population variation in nest building behaviors of Bornean orangutans (*Pongo pygmaeus wurmbii*): individual plasticity and cultural influences.

The aim of this chapter was to investigate the effect of social barriers, as well as other factors that may limit the spread of knowledge, skills and innovations in the nest-building context within orangutan population. Orangutans spend the night in self-made nests they build every day. Nest building is a socially learned skill that requires extensive practice. In fact, after feeding, nest building is the most peered-at behavior by immature orangutans. Peering, which is a proxy for social learning in orangutans, decreases rapidly with age and becomes very rare once individuals reach reproductive age. The nesting repertoires are thus not expected to substantially expand in mature individuals other than through independent modifications and innovations. There is a little potential for social transmission of these rare, non-subsistence, comfort-related innovations among adult orangutans. As such it is likely that the nest building repertoire of the individual is similar to that of its mother and local patterns in these repertoires could therefore potentially show a strict matrilineal signal.

We investigated local variability in nest building behaviors of Tuanan orangutans to infer the size of the cultural unit in this species. We compared nesting repertoires of resident individuals (females) with immigrants (males) as well as related and unrelated females and linked dyadic similarities to patterns in genetic relatedness, social exposure and home range overlap. Differences between males and females would suggest that the unit is smaller than dispersal distance and differences between unrelated females would suggests that the cultural

unit is smaller and there is an effect of social barriers within the population that limits the spread of behavioral variants.

We could show that orangutans have a very broad nesting repertoire and enormous flexibility in combining a variety of different element models into unique nest architectures. As the skilled nest builders they are, they can make use of many tree species and tree architecture types to build the nest. Yet, we also show clear preferences in both choice of nest tree species and use of different nest elements and their models. The results of our study show that most of the nest-related behaviors and choices surrounding nesting are customary among all the members of the population (i.e. the tree species, nest position choice, model of platform built, foundation used, production of nest-specific vocalizations, and twig biting and smoothing), while others can be limited and spread within smaller units (i.e. leaf carrying of *Campnosperma coriaceum*). We therefore suggest that different behaviors may spread differently within the population and thus the size of cultural unit varies depending on the behavior in question.

Overall, we found little within-population variation in cultural repertoires, despite what seemed to be clear social barriers among the females. Further investigation of the role of males in spread of knowledge acting as vectors of transmission is required to evaluate how certain cultural variants that are known to differ between populations become universal at the population level and are similar for both sexes (Mörchen 2016).

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Chapter 2: When is necessity the mother of invention? – Testing innovation in reintroduced Bornean orangutans (*Pongo pygmaeus*)

Anna Marzec, Benjamin Laubi, Denny Kurniawan, Sri Suci Utami Atmoko, Erik P. Willems, Maria A. van Noordwijk, Carel P. van Schaik

Abstract

Wild orangutans exhibit strong neophobia and little independent exploration, but acquire vital skills socially from their mothers and others when young; thus, innovations are rare, but once made, tend to be retained in the population. Here, we investigate whether reintroduction of ex-captive mature animals into a novel habitat elicits more exploration and innovation than observed in a well-studied wild population of Bornean orangutans (*Pongo pygmaeus*). We examined the dynamics in diet composition and breadth, and the main mechanisms of acquisition: social learning and independent exploration. We found that reintroduced individuals showed higher rates of peering (an index of social learning) and far higher rates of independent exploration than wild orangutans did, and initially had far broader diets as a result. In addition, the intensity of learning both individually and socially decreased over time. Thus, reintroduced mature orangutans need to acquire the necessary skills and knowledge to survive post release, and rely on a mix of solitary and social learning to do so. Our results therefore suggest that necessity can make orangutans in nature go beyond the regular orientation toward social learning and also become far more exploratory. Because our ancestors probably were far less curious and innovative than modern humans are, necessity may likewise have elicited the unusual curiosity of humans.

Introduction

Humans are the most innovative species in the animal kingdom, with high and steadily rising rates of exploration and innovation. However, the paleoanthropological record implies that our ancestors were much less innovative and creative than modern humans are (Durham 1991, Tennie et al. 2017) suggesting that a change toward curiosity happened sometime during human evolution. Research on animal innovation may therefore help to understand the processes behind the origin and later development in creativity and innovativeness in our ancestors.

The process of innovation is a driver of cultural change. An innovation is a novel behavior that is not acquired reliably by each member of a population during development, nor appears reliably in response to particular ecological or social conditions (Reader and Laland 2003). Although innovations may be independently acquired by more than one individual (Ramsey et al. 2007, van Schaik et al. 2016), they more often spread socially, through either copying or more commonly socially mediated re-innovation, so some become customary, i.e. are frequently observed in most individuals of the same population. Most innovations are therefore identified through comparisons of populations, which often yield a particular behavior being common in one population but absent in others despite occupying similar habitat and/or having access to the same substrates. A classic example of such innovations can be tool use in feeding contexts (e.g. Boesch et al. 1994, Ottoni and Izar 2008, van Schaik et al. 2003), or dietary differences between populations (e.g. Bastian et al. 2010, Chapman and Fedigan 1990, van de Waal et al. 2017).

Although there is a literature on observed innovations in birds (Lefebvre et al. 2004) and therefore of pathways toward innovation (Griffin and Guez 2014), reports documenting the actual occurrence of an innovation and its subsequent fate among primates are surprisingly rare, even from long-term studies (Japanese macaques: Leca et al. 2007; chimpanzees: Yamamoto et al. 2008, Hobaiter et al. 2014; capuchin monkeys: Perry et al. 2017). Because of this, primate innovations are mainly documented using indirect methods (Whiten et al. 1999, Fragaszy and Perry 2003, van Schaik et al. 2006, Krützen et al. 2007), and therefore not much is known about conditions under which innovations arise in the wild. van Schaik et al. (2016, see also Kummer and Goodall 1985) recognize six pathways for how innovations may arise: (1) response to novelty, (2) finding a new solution to an old problem, (3) accidental innovation, (4) goal-directed problem solving, (5) necessity and (6) curiosity (see also Reader et al. [2016] for a more bird-oriented approach). It has been suggested that goal-directed exploration in order to

solve a new problem (e.g. gain access to an inaccessible known food source) seems to be most likely mechanisms at work in non-human primates while others are rather incidental (van Schaik et al. 2016). Systematic work on orangutans, chimpanzees and capuchin monkeys yielded precious little evidence for increased exploration in times of food scarcity or in populations in the poorest habitats, suggesting that necessity plays a marginal role in innovation (Koops et al. 2013, 2014, cf. van Schaik et al. 2016). However, some chimpanzee data suggest otherwise (Yamakoshi and Sugiyama 1995, Gruber et al. 2012, Grund et al. 2019). This variability suggests there may be some conditions that unleash innovations. Here, we revisit the role of necessity in orangutan innovation using a different approach, namely by studying ex-captive, reintroduced orangutans.

Orangutans are semi-solitary, long-lived, large-brained, arboreal apes with extensive cultural repertoires. Females of this species have the longest known birth intervals among all mammals (on average 7.6 years: van Noordwijk et al. 2018). Immatures stay in constant association with their mothers until a few years after the next offspring is born, and during this time learn from them all necessary skills, including the diet (Jaeggi et al. 2010, Schuppli et al. 2016). They peer (i.e. intently watch another individual's activity from a close distance) and subsequently engage in peering-induced exploration, and thus rarely engage in independent exploration. Exploration rates decrease with age, reaching very low values in adulthood (Schuppli et al. 2016). After being weaned, immatures enter the most social phase of their life and associate more with peers and other members of the population, thus gaining additional opportunities to learn from others than just their mother. Upon reaching maturity, associations between same-sex individuals are generally rare, but there are significant differences in gregariousness between populations within and between orangutan species.

As a result, under natural conditions, mature orangutans rely almost completely on the knowledge acquired socially during infancy and juvenility and show a high level of neophobia (Forss et al. 2015). Given their solitary lifestyle and the females' preference for associating with female relatives (van Noordwijk et al. 2012), the actual opportunities for social learning in adult life are very limited. Nonetheless, important innovations, even though rare, once made are likely to be retained in the population thanks to social transmission mostly from mother to offspring. As a result, orangutans have rich behavioral repertoires (Bastian et al. 2012, van Schaik et al. 2016).

Interestingly, the novelty-averse and non-explorative orangutans as we know them from the wild behave differently in captive settings. The phenomenon of the so-called 'captivity

effect' has been observed in many primates (Halsey et al. 2006, Haslam 2013) but is particularly pronounced in orangutans (Damerius et al. 2017a, Forss et al. 2015, Hardus et al. 2015). When comparing different prerequisites for solitary and social learning in wild and captive individuals a striking contrast emerges (table 1). Wild orangutans are highly neophobic. They are known to be reluctant to touch or even approach novel food and objects for months (Forss et al. 2015) and rely mostly on socially induced rather than independent exploration. In contrast, captive orangutans are known for their innovations and quick individual learning through independent exploration and trial and error (Russon et al. 2009a). They are also among the best problem-solvers (Lethmate 1982, Damerius et al. 2017b). Moreover, captive orangutans have more opportunities to learn socially, not only from conspecifics they are housed with but also from human role models. Finally, they remain active learners far into adulthood (Lehner et al. 2011). It has been shown that reduced neophobia and increased curiosity are induced by safe environment and (perhaps most importantly) contact with humans (Damerius et al. 2017a).

These results show that although orangutans have great abilities to innovate, this potential is not expressed under natural conditions. Here, we test under which conditions in nature orangutans can be innovative, by using the natural experiment of an ongoing reintroduction project of ex-captive orangutans. It is meant to solve the conundrum of the major differences in how orangutans learn under natural vs. captive conditions.

Table 1. Captivity effect in orangutans.

Rate/level of	Wild orangutans	Captive orangutans
Exploration rate	Low	High
Innovation rate	Low	High
Curiosity	Low	High
Neophobia	High	Low
Sociality	Low	High

Reintroduction, defined in the IUCN guidelines (2013) as "the intentional movement and the release of an organism inside its indigenous range from which it disappeared," is now a widespread conservation tool (Seddon et al. 2007). Moving any individuals from their familiar habitat and releasing them into a new, unknown one and without knowledgeable conspecifics bears a high risk of failure. Especially for these species that under natural conditions must learn ecological skills such as diet, and do so socially. As such, reintroduction efforts can be seen as a natural experiment that provides an opportunity to study how orangutans learn skills needed

for survival in habitat that is new to them. In particular, we ask whether in this situation, where there are only limited opportunities, if at all, for socially guided skill acquisition, necessity induces them to innovate.

We predict that mature individuals reintroduced into a new environment will have both a greater tendency to explore (measured through rates of exploratory behaviors) the environment and a greater interest in social learning (measured through peering rates) than their conspecifics in wild populations. In addition, we predict that the longer the individuals have spent in new environment, and the more familiar they therefore have become with it, the less they need to learn both socially and through independent exploration. We evaluate the efficiency of learning by looking at the size and composition of the diet of reintroduced individuals. We predict that newly reintroduced orangutans, since they have little knowledge about their environment will feed less on high-quality food such as fruits compare to wild conspecifics. However, we also predict that once individuals have spent longer in this habitat and thus have acquired more knowledge, their diet composition will become more similar to that of wild orangutans. Finally, we expect that reintroduced orangutans try out and feed on many food items before they settle on their diet. As a result, they will have broader diets and feed on more different food items (plant species-organ combinations) per unit time than wild orangutans do.

To test these predictions, we make use of the 'natural experiment' of the reintroduction of ex-captive Bornean orangutans that were released into a new habitat in which they did not grow up and thus could not have assembled an appropriate skill set for. Reintroduced orangutans differ in rehabilitation history and could be followed over different phases post-release. In order to test the prediction, we collected data on diet and all learning-related behaviors (independent exploratory behaviors and peering) as well as their sociality (time spent in associations and identity of social partners). This study was conducted in Bukit Batikap release site in Central Kalimantan. We used long-term data from the Tuanan Orangutan Research Project (TORP) for the comparison with wild orangutan population.

Methods

Study sites

We collected data on Bornean orangutans from two populations in Central Kalimantan in Indonesia: (1) an artificially created 'population', reintroduced by Borneo Orangutan

Survival Foundation (BOSF) population in Bukit Batikap, and (2) the wild population of well-studied orangutans in Tuanan, about 250 km to the South.

The Batikap release site (0º40′S, 114º03′E) is located within the Bukit Batikap Conservation Forest in Murung Raya district. The research area covers ca. 8000 ha and consists of almost undisturbed lowland (200-500 m asl), mixed dipterocarp forest with patches of heath forest and strips of riparian forest along the rivers with, in a few locations, secondary regrowth from historical crop cultivation (Husson et al. 2012). As stipulated by the IUCN guidelines (2013) the area is not currently inhabited by a natural population of orangutans. The release site is isolated and away from human settlements. The reintroduction efforts at this site began in 2012, and 150 individuals had been reintroduced before the start of data collection. Data were collected from May 2016 to March 2017 on 10 ex-captive, mature female orangutans released between 2012-2016 (table s9).

For comparison we used data collected within Tuanan Orangutan Research Project (2°15′ S, 114°44′ E) situated in the Mawas Reserve. The research area consists of 750 ha of low-altitude (<5 m asl) peat-swamp forest, selectively logged in the 1990s and recovering since. With approximately 4.5 ind/ km^2 (van Schaik et al. 2005), the orangutan density is among the highest in Borneo (Husson et al. 2009) This population has been intensively studied since 2003 and the social relationships and relatedness among the individuals are largely known (Arora et al. 2012, van Noordwijk et al. 2012). Data from 10 mature females (table s9) from three different matrilines collected between August 2010 and August 2015 were used for comparison.

Reintroduced individuals

The reintroduced females differ in their background and rehabilitation history. The differences included estimated age at arrival in the center, time spent in captivity, extend and intensity of human contact, type of rehabilitation process subjected to, as well as time in the new habitat since the release (table s10). Prior the release, the individuals were all housed and cared for by BOSF in the Nyaru Menteng Rehabilitation Center for several years. All of the individuals were young and without their mothers at the time of confiscation. Basic information about the individual condition, place of origin as well as age estimates was collected, but data on the duration of stay in captivity and the conditions prior to confiscation is often unreliable, because the orangutan is a protected species and its possession is illegal. To account for the individual variation among the reintroduced orangutans we classified them into two main

categories (table 2), depending on their pre-release experience (full versus partial rehabilitation) and on the time they had spent in new habitat post-release (novice versus experienced).

Table 2. The categories and subcategories of pre- and post- release experience of reintroduced individuals (for a list of individuals and details, see table s10).

Category	Subcategory	Definition	Individuals
Experience (post-release)	Novice	Individuals who, at the beginning of the study, spent <14 months in new habitat since their release	6
	Experienced	Individuals with ≥2.5 years in the new habitat since their release	4
Rehabilitation (pre-release)	Full	Individuals who were estimated to be <3 years old when captured and separated from their mothers, extensive contact with humans, and >10 years in rehabilitation	4
	Partial	Individuals estimated to be ≥3 years old when captured and separated from their mothers, less contact with humans, and <10 years in rehabilitation	6

The goal of the rehabilitation is to prepare orangutans for the independent life back in their natural habitat. Therefore, orangutan rehabilitation and reintroduction is considered successful if the released individual survives in the new habitat on its own without human support.

Data collection

We matched the available focal individuals at Batikap with similar ones from the much larger data set for Tuanan. Orangutans were followed during all-day follows, whenever possible for a maximum of five (in Batikap) and ten (in Tuanan) consecutive days per month, using focal animal sampling following standardized protocols (cf. van Schaik 1999, http://www.aim.uzh.ch/research/orangutannetwork/sfm.html). All observers were well-trained and frequently conducted inter-observer reliability tests. Moreover, two of the observers collected data at both sites. For all analyses involving rare behaviors, we used a restricted data set from Tuanan, i.e. data collected by selected observers who in particular focused on social interactions and exploratory behaviors and had sufficient inter-observer reliability (IOR) scores (Cohen's Kappa ≥ 0.91).

Analyses

For all the analyses we used data from the same mature females from each site with a minimum of 150 observation hours: ten wild and nine reintroduced (see table s9). One reintroduced female (Jambi), who died from unknown cause early during the data collection, and for which we did not reach the threshold of minimum observation hours, was excluded from all the analyses. Due to differences in the length of follow days at each site, for the general analysis of activity budget and diet composition we used only data collected from 9 AM onwards from both sites to avoid any effects of time of day. In addition, we excluded all follow days shorter than 3h and individual's monthly samples if less than 12h. For the analyses on learning behaviors we used all data collected continuously during focal follows longer than 3h. For this analysis, we restricted the Tuanan data set to selected observers who focused on learning behaviors and had sufficient IOR scores in recording rare behaviors.

All analyses were performed in R (version 3.4.3) using the lme4 package (Bates et al. 2014). Data were analyzed using Poisson generalized linear mixed models (GLMM) which included the number of observation minutes as a ln-transformed offset, and individual identity as a random factor, given that data contained multiple observations on the same individuals and sampling effort was not equal across animals. We used data collected on wild orangutans (i.e. Tuanan dataset) to determine whether to include Fruit Availability Index (FAI, see table 3) and class (i.e. mother or non-mother) as fixed effects in the model. Age was not tested, due to the fact, that in the wild population age was confounded with class (mothers were necessarily older females while non-mothers – young, nulliparous females). Since there was no significant effect of class within the wild population we did not include it as fixed effect in further analysis. FAI, however, often did have a significant effect and as such was included in all the analysis.

For each prediction we performed a two-stage comparison, which allowed us to include all relevant fixed effects. In the first stage (I), we investigated whether there was a difference between wild orangutans on the one hand, and both novice and experienced reintroduced orangutans on the other (i.e. two contrasts with wild orangutans set as the reference category). In the second stage (II), we focussed our analyses on rehabilitant orangutans only to investigate the effect of post-release experience while controlling for pre-release experience. Since it has been shown, for many species including orangutans, that an individual's early-life experience has a lasting influence on its exploratory tendencies (Damerius et al. 2017a, reviewed in Reader 2015, Riedler et al. 2010), we therefore include rehabilitation category, i.e. the pre-release, in-captivity experience, as a fixed effect, as it is likely to influence the individual's previous

knowledge and/or preference for how it learns. Each variable of interest was expressed as a function of the same set of fixed effects (table 3) and we always reported the results of the full model. To assess model significance, we compared the full model to a null model consisting of the intercept and the random effect. Due to differences in overall productivity of two habitats a scaled (converted to z-scores) FAI index was used whenever analysis included individuals from both populations. Visual inspection of the residual plots did not reveal any obvious deviations from homoscedasticity or normality.

Table 3. Description of all fixed effects used in the analysis.

Fixed effect	Description	Levels	Stage
Group	Individuals are categorized into one of the three groups depending on extent of experience in living under natural conditions: (1) wild orangutans, (2) reintroduced experienced, and (3) reintroduced novice individuals. Wild orangutans are set as contrast and the model compares each reintroduced group to the wild individuals.	3	I
FAI	Fruit availability index, i.e. percentage of trees bearing fruits in the phenology plots. For these analysis where data from both sites were included the FAI was scaled.	continuous	I and II
Experience	We categorize reintroduced individuals depending on the time spent in the new habitat since release as either novice or experienced (see table 2).	2	II
Rehabilitation	We categorize individuals as partially or fully rehabilitated depending on the time and type of rehabilitation they were subjected to (see table 2).	2	II

Results

We predicted that both 1) social and 2) individual learning will be more frequent in both groups of reintroduced compared to the wild orangutans. In addition, we expected it to be also more frequent in newly reintroduced individuals (novice) than these who spent over 2.5 year in the new habitat since their reintroduction (experienced).

Social learning

Being in association with another individual is a necessary pre-condition for social learning to occur. Therefore, we first looked at time spent in association by wild compared to both experienced and novice reintroduced females. In order to account for individual variation,

we used counts of minutes spent by focal females in association with mature individuals each month. Against our expectation there was no difference between wild and experienced reintroduced individuals (GLMM, Experienced vs. wild: β= -1.13, z= -0.982, p=0.326), nor between wild and newly reintroduced individuals (GLMM, Novice vs. wild: β= -1.5, z= -1.395, p=0.163). Only the fruit availability index (FAI) had a significant positive effect on time spent in association (table 4). Interestingly, wild females spent more than half of their association time (on average 57% ±12% SE) with males, whereas experienced and novice reintroduced females only spent on average 28% ± 24% SE and 27% ± 16% SE, respectively, in mixed-sex associations.

Experience did not have a significant effect on time spent in association within reintroduced orangutans (GLMM, Experience (novice): β= -0.93, z= -0.524, p=0.600). Also, no rehabilitation effect was found. However, FAI did have a positive significant effect (Table 5).

Next, we looked at peering as an index of social learning (see Schuppli et al. 2016). Since under natural conditions peering among adults may also have a social function of testing social tolerance, only food-related peering events were included. We used total counts of food peering events per month for all the females who were observed in association with other mature individual(s) and therefore had an opportunity to peer: ten wild and eight reintroduced individuals (fig.1). Our results supported the prediction: Both reintroduced groups peered significantly more in the feeding context at their association partner than their matched wild counterparts did (GLMM: Novice vs. wild: β= 3.04, z= 5.711, p<0.001; Experienced vs. wild: β= 1.85, z= 2.914, p=0.004; table s1).

Table 4. Results of full GLMM for stage I comparison with counts of minutes spent in association per month per individual as an outcome (N=153), with wild orangutans set as the reference category, individual as random effect and ln-transformed monthly observation time as an offset.

Response	Effect	Effect type	Estimate	Std. Error	z value	P-value	N (153)
Count of minutes in association/ month	(Intercept)	Fixed	2.51	0.61			
	Experienced vs. wild	Fixed	-1.13	1.15	-0.982	0.326	2
	Novice vs. wild	Fixed	-1.50	1.08	-1.395	0.163	2
	FAI scaled	Fixed	0.11	0.00	24.612	**<0.001**	cont.
	Log (time observed/month)	Offset	-	-		-	cont.
	Individual	Random	-	-		-	19
$\chi^2_{(2,5)} = 595.65$, p<0.001)							

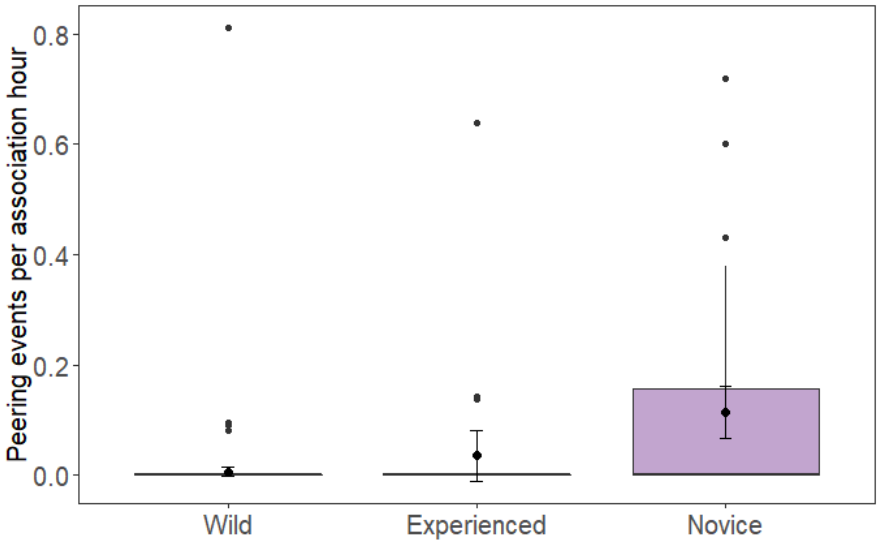
Table 5. Results of full GLMM for stage II comparison with counts of minutes spent in association per month per individual as an outcome (N=72), individual as random effect and ln-transformed monthly observation time as an offset.

Response	Effect	Effect type	Estimate	Std. Error	z values	P-value	N (72)
Count of minutes in association/ month (Full model:	(Intercept)	-	2.51	0.61			-
	Experience (novice)	Fixed	-0.93	1.78	-0.524	0.600	2
	FAI	Fixed	0.17	0.01	13.518	**<0.001**	cont.
	Rehabilitation (partial)	Fixed	-2.60	1.87	-1.390	0.163	2
	Log (time observed/month)	Offset	-	-		-	cont.
	Individual	Random	-	-		-	9
$\chi^2_{2,5}$= 178.66, p<0.001)							

With the same approach, using monthly counts of food-related peering events per individual, we tested whether experience had an effect on peering in reintroduced orangutans. Our result did support the prediction that newly released individuals peered significantly more than experienced ones (GLMM, Experience (novice): β= 1.26, z= 2.647, p=0.008; table s2)

We also examined the direction of all food-related peering events among reintroduced individuals, recorded during focal follows in which a focal individual was involved as either peerer or demonstrator (N=62). The prediction here was, that if peering indeed serves a learning purpose, individuals with less experience will peer at more experienced ones. The order of release within each dyad was therefore considered, i.e. whether the peerer was released at the same time, earlier or later than the demonstrator was. The great majority (90%) of associations and therefore opportunities for peering were between individuals with a different level of experience, while 10% of associations was between individuals reintroduced at the same time. In fact, all food related peering events took place in mixed-experience associations, and none were recorded between individuals of equal experience. In mixed-experience association the probability of peering at more experienced individuals (N=46) was 74% (95% CI, 61-84%), compared to 26% (95% CI, 15-38%) of peering in opposite direction (N=16). This difference was significantly above chance, binominal test p= 0.0002. As predicted, individuals released later and therefore with less experience peered nearly three times more at more experienced partners than vice versa.

Fig.1 Food-oriented peering rates by each group: wild, experienced reintroduced, and novice reintroduced orangutans.

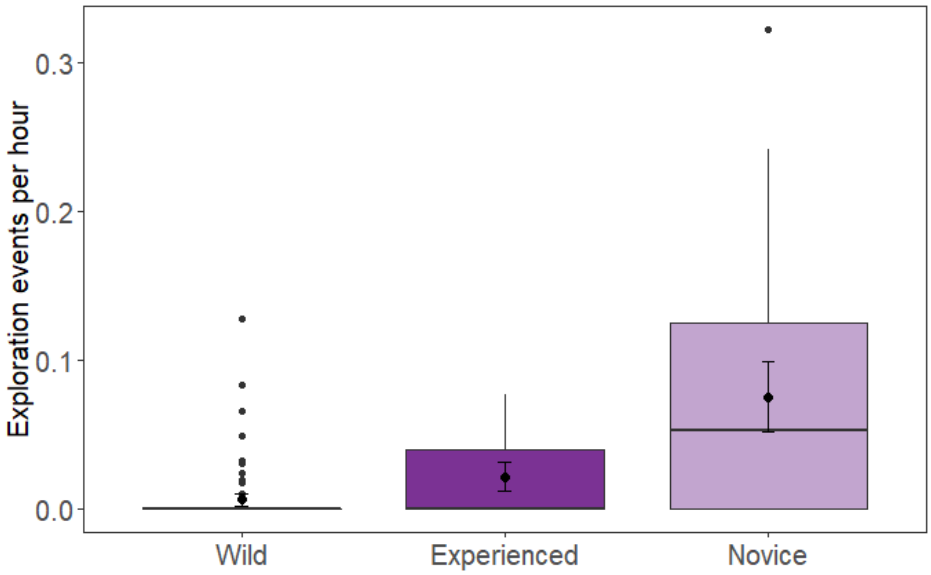


Individual learning

Exploratory behaviors such as try feeding (i.e. tasting food items without ingesting them) and object manipulation were used as an index of individual learning. In total, for all individuals of both populations included in the analysis, we recorded 185 exploratory behaviors. The overwhelming majority, 78% (N=144) were observed in reintroduced orangutans: on average 20.6 ±21.2 SD per novice, and 10.25 ±4.6 SD per experienced individual compared with on average 4 ±7.2 SD exploratory behaviors per wild orangutan. Since not all exploratory behaviors were food oriented we considered only those that occurred in the feeding context. While in wild orangutans only 40% of total exploratory behaviors were food oriented (N=16; on average 1.6 ±2.7 SD per individual), in the experienced reintroduced orangutans it was 54% (N=22; on average 5.5 ±2.4 SD per individual) and in novices as much as 68% (N=70; on average 14 ±12.9 SD per individual). In order to account for individual variation, we ran a GLMM using counts of food oriented exploratory behaviors per month for each focal female (fig.2). The results of the model showed that reintroduced experienced orangutans explored significantly more in the feeding context than wild orangutans (GLMM, Experienced vs. wild: β= 1.59, z= 2.595, p=0.009). The same was true for novice orangutans, for whom the effect was even stronger (GLMM, Novice vs. wild: β= 2.62, z= 4.728, p<0.001; table s3). There was also a significant effect of novices exploring more in the feeding context

than experienced reintroduced females (GLMM, Experience (novice): β= 0.98, z= 2.252, p=0.012; table s4).

Fig.2 Food-oriented exploration rates by each group: wild, experienced reintroduced, and novice reintroduced orangutans.



Diet

To evaluate the overall effect of both solitary and social learning we looked at feeding time and diet composition. We predicted that novice and experienced reintroduced orangutans would feed less on high-quality food, i.e. fruits, and more on fallback foods, such as bark and pith, than wild individuals. In addition, we predicted bigger overall diet repertoires and higher number of item-species combination eaten per unit time in both groups of reintroduced than in wild individuals. Within reintroduced individuals we expected an increase in the time spent feeding on fruits as well as a decrease in the number of item-species combinations consumed per unit time in experienced individuals compared to novices.

First, we tested whether each orangutan category spent the same amount of time feeding. Both categories of reintroduced individuals spent significantly more time feeding per month (GLMM, Experience vs. wild: β=0.14, z= 2.709, p= 0.007; Novice vs. wild: β=0.26, z= 5.571, p<0.001; table 6) than wild orangutans did. In addition, novices spent significantly more time feeding than experienced reintroduced females (GLMM, Experience (novice): β=0.11, z= 7.441 p<0.001; table 7). For the analysis of diet composition i.e. time spent feeding on fruits (fr), bark

(bk) and pith, we used minutes spent feeding per month on each food item and used total monthly feeding time as an offset. Our result supported the prediction: reintroduced novice and experienced individuals spent significantly less time feeding on fruits (GLMM, Experience vs. wild: β_{FR}= -0.46, z= -5.88, p<0.001; Novice vs. wild: β_{FR}= -0.89, z= -12.14, p<0.001) and significantly more time feeding on bark (GLMM, Experience vs. wild: β_{BK}= 1.75, z= 7.392, p<0.001; Novice vs. wild: β_{BK}= 1.79, z= 8.160, p<0.001) as well as pith (GLMM, Experience vs. wild: β_{PITH}= 2.30, z= 8.133, p<0.001; Novice vs. wild: β_{PITH}= 2.40, z= 9.172, p<0.001) than wild orangutans (fig.3). In addition, FAI had a significant effect on time spent feeding on all items (table s5).

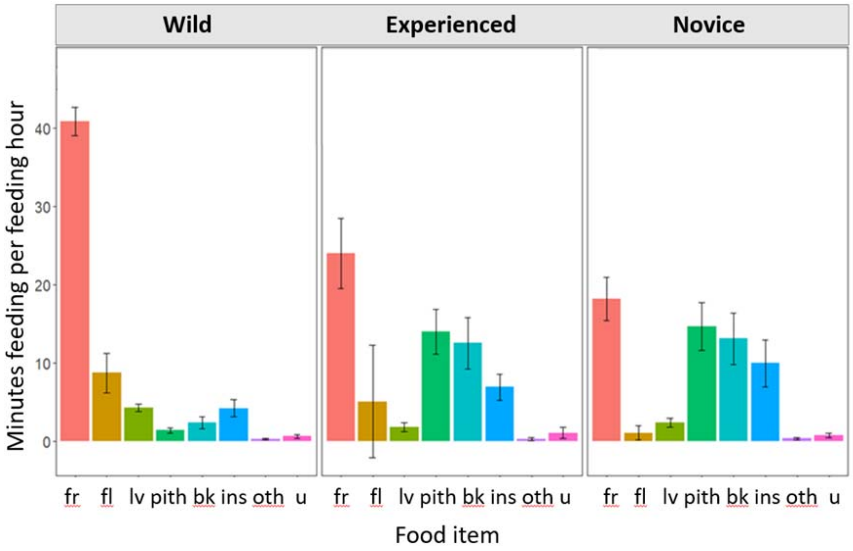
Table 6. Results of full GLMM for stage I comparison with minutes spent feeding per month as an outcome (N=246), with wild orangutans set as the reference category, individual as random effect and ln-transformed monthly observation time as an offset.

Response	Effect	Effect type	Estimate	Std-Error	z values	P-value	N (246)
Minutes feeding/ month	(Intercept)	Fixed	3.48	0.03			
	Experienced vs. wild	Fixed	0.14	0.05	2.709	**0.007**	2
	Novice vs. wild	Fixed	0.26	0.05	5.571	**<0.001**	2
	FAI scaled	Fixed	-0.02	0.00	-9.968	**<0.001**	cont.
	Log (follow time a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-		-	19
$\chi^2_{(2,5)}$=118.91, p<0.001							

Table 7. Results of full GLMM for stage II comparison with minutes spent feeding per month as an outcome (N=65), with individual as random effect and ln-transformed monthly observation time as an offset.

Response	Effect	Effect type	Estimate	Std-Error	z values	P-value	N (65)
Minutes feeding/ month	(Intercept)	-	3.55	0.02			
	Experience (novice)	Fixed	0.11	0.01	7.441	**<0.001**	2
	FAI	Fixed	0.06	0.01	10.386	**<0.001**	2
	Rehabilitation (partial)	Fixed	-0.01	0.02	-0.401	0.688	cont.
	Log (follow time a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-		-	9
$\chi^2_{(2,5)}$=122.41, p<0.001							

Fig.3 Minutes per feeding hour spent feeding on different items by each group: wild, experienced reintroduced, and novice reintroduced orangutans.



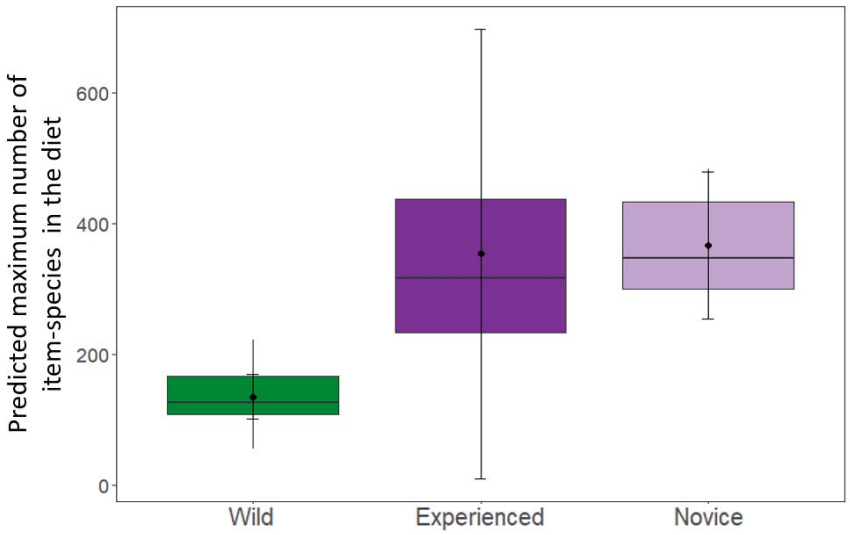
Moreover, as predicted, novice reintroduced individuals spent less time feeding on fruit (GLMM, Experience (novice): β= -0.36, z= -4.378, p<0.001) than experienced females did. However, there was no experience effect on time spent feeding on either bark (GLMM, Experience (novice): β= 0.12, z= 0.600, p=0.548) or pith (GLMM, Experience (novice): β= -0.06, z= -0.124, p=0.901). Interestingly, both FAI and rehabilitation did have significant effect on time spent feeding on all items (table s6).

Diet breadth

In order to compare overall diet breadth of each experience category of reintroduced orangutans versus wild individuals as well as between the experience categories, we calculated the maximum predicted diet size for each individual using the cumulated saturation curves with a fitted Michaelis-Menten model, where K is the time needed to reach half of the predicted maximum diet (V_{max}). The mean maximum predicted diet size, in item-species combinations, for both novice ($V_{max\ Novice}$= 367 ± 91 SD, K = 118.7 ± 58.1 SD) and experienced reintroduced orangutans ($V_{max\ Experienced}$= 354 ± 216 SD, K = 234.5 ± 143.8 SD) was more than twice as high as in wild individuals ($V_{max\ Wild}$= 136±48 SD, K = 126.0±77.5 SD). The difference between the groups was significant Kruskal-Wallis: $\chi^2_{(2)}$= 11.46, p= 0.003 (fig.4). The results of post-hoc pairwise comparison using Wilcoxon rank sum test with corrections for multiple testing showed that only wild vs. experienced (p=0.036) and wild vs. novice (p=0.002) were significantly different, confirming the prediction. However, against our expectation, there was no difference

between experienced and novice (p=0.730). We also calculated saturation rates (Sr= (V_{max}/2)/K) in order to evaluate how frequently new item-species combinations were added into the diet. As expected, novice reintroduced individuals had the highest saturation rate of, on average, 1.7 ± 0.6 SD item-species/hour while experienced reintroduced and wild orangutans much showed lower saturation rates of 0.8 ± 0.1 SD and 0.8 ± 0.5 SD item-species/hour respectively (fig.5). Results of Kruskal-Wallis rank sum test confirmed that the difference in saturation rates between the groups was significant ($\chi^2_{(2)}$= 8.06, p= 0.018). Post-hoc pairwise comparison using Wilcoxon rank sum test with corrections for multiple testing showed that there was no significant difference in saturation rates between wild vs. experienced (p= 0.374) while the difference was significant for wild vs. novice (p=0.024) as well as between experienced and novice (p=0.024).

Fig.4 Maximum predicted diet size (number of item-species combinations eaten) calculated using individuals' cumulated saturation curves with fitted Michaelis-Menten models, grouped by wild, experienced reintroduced, and novice reintroduced orangutans.



In addition, we compared the count of item-species eaten per feeding hour per day between the two experience categories of reintroduced orangutans to their wild conspecifics (fig.6). The results were consistent with results comparing saturation rates. There was no significant difference between experienced reintroduced and the wild orangutans (GLMM, Experience vs. wild: β= 0.06, z= 0.950, p=0.342) while novices fed on significantly more item-species per feeding hour per day than wild individuals (GLMM, Novice vs. wild: β= 0.30, z= 5.210, p<0.001). Not surprisingly, FAI also had an effect (table s7). Within reintroduced

orangutans, as expected, novices fed on significantly more item-species per feeding hour per day (GLMM, Experience (novice): $\beta = 0.27$, $z = 3.474$, $p < 0.001$; table s8).

Fig.5 Diet saturation rate of each group: wild, experienced reintroduced, and novice reintroduced orangutans.

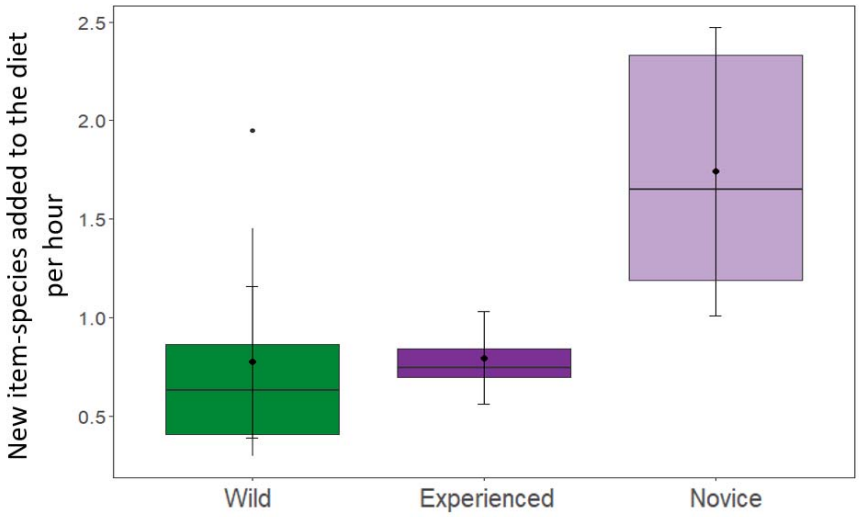
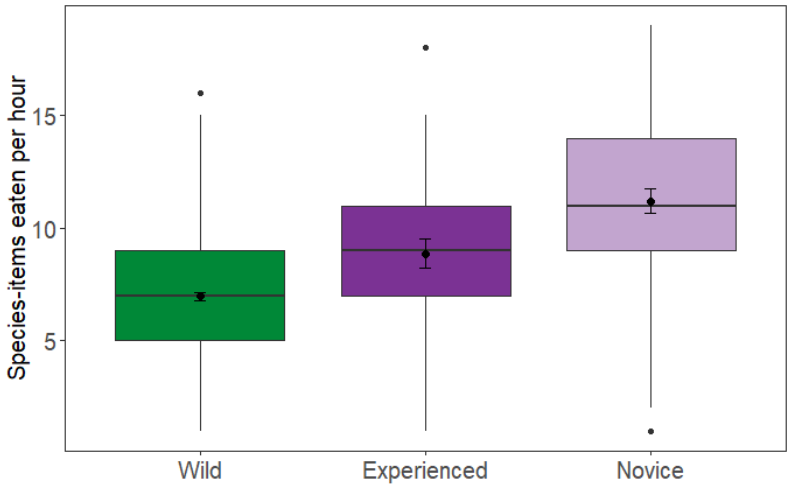


Fig.6 Number of item-species combinations eaten per hour by wild, experienced reintroduced and novice reintroduced orangutans.



Discussion

Orangutan reintroduction allows us to study this species under experimental conditions. Ecologically naïve mature individuals are moved into a habitat that is new to them, where they need to acquire essential knowledge in order to survive. Our study shows that these reintroduced

orangutans use a mix of social learning by peering and independent learning by exploring to acquire the necessary new knowledge. The significantly lower frequency of these behaviors in experienced reintroduced orangutans relative to the novices suggest that the intensity of learning decreases as the necessity diminishes. We demonstrated, using diet as an example, that with experience, reintroduced individuals acquire skills and knowledge, and as a result become more similar to wild orangutans.

In the wild, orangutans learn all the necessary knowledge socially from the mother and others through observation i.e. peering, followed by selective exploration and repeated practice. Upon reaching maturity, peering is rare and may serve a social more than a learning function (Schuppli et al. 2016). However, in the reintroduced individuals, we observed much higher food-oriented peering rates between mature individuals than in the wild population even though the time spent in association did not differ. Lower peering rates, without a concomitant decline in time spent in association, in experienced compared to novice reintroduced orangutans suggest that the need for social learning decreases as the individual's knowledge base increases. Therefore, the intensity of learning depends on the degree of necessity.

Previous studies on rehabilitant great apes showed that survival competencies, measured in behavioral changes post-release, require learning, much of which is reflected in experience (Hannah and McGrew 1991, Ongman et al. 2013, Russon 2002, 2003, 2009, Grundmann 2006, Russon et al. 2007). In our study, we showed that reintroduced orangutans selectively pick knowledgeable (i.e. more experienced) role models for social learning rather than other, equally naïve individuals. Similar, albeit anecdotal observations were reported for orangutans reintroduced in Meratus, East Kalimantan (Grundmann 2006). These findings suggest they are capable of assessing skill levels of associates, rather than relying on a simple rule, such as attend to older individuals. Human children appear to use very similar decision rules (Harris 2012).

Custance et al. (2002) likewise suggested enhanced social learning effects in primates when they were presented with a knowledgeable demonstrator. In fact, it has been recommended to introduce naïve individuals together with experienced ones (Stoinski et al. 2003). These effects of associating with knowledgeable conspecifics may well extend beyond primates. For instance, reintroduced captive-born Vancouver Island marmots (*Marmota vancouverensis*) effectively used wild individuals to gain foraging skills experience (Lloyd et al. 2019).

Nonetheless, like their wild conspecifics, the reintroduced orangutans are semi-solitary and as such still spent the majority of time on their own, and in addition their role models are

themselves still learning. Thus, social learning alone is probably not enough to acquire all needed knowledge and thus solitary learning through exploration and trial-and-error is expected to play an important role. Indeed, we could show that reintroduced orangutans explore more than their wild conspecifics. Similarly, reintroduced captive-born golden lion tamarins were more exploratory, showing higher rates of micromanipulation in foraging context than wild born, more knowledgeable individuals (Stoinski et al. 2003). Since exploration may be harmful and may result in injury or poisoning (Hart 1993, Milinski 1993), for animals with a slow life history it is normally safer to avoid novelty and the potential risks associated with it.

Reintroduced into new, unknown habitat, ex-captive orangutans face a necessity to learn how to survive, balancing costs and benefits of exploration. They need to explore in order to learn for example what to feed on, yet they have to do it carefully to avoid the potential danger. Food oriented exploration such as try-feeding allows individuals to sample different foods and results in assembling the diet. The more food is being sampled the higher the chances of including valuable food source in the diet. However, try-feeding may come at high cost since some species or particular items of certain species are poisonous. It has been observed, that after illness presumably caused by feeding errors, one initially very exploratory orangutan became reluctant to explore and therefore learn (Nayasilana et al. 2017) and eventually died (S. Husson pers.com). Unfortunately, the data on orangutan survival rates post-release remain to be analyzed. However, the impression is that most of recorded cases of death and sickness in reintroduced population of orangutans in Batikap (AM pers. obs.) and Bukit Baka Bukit Raya (S. Husson, pers. com.) happen in the first year after release when individuals have still limited knowledge. In our study, the female Jambi, who was excluded from the analysis, died during the first year after release. Although the cause of her death was not identified, she was never observed to explore or peer in the feeding context (table s9). Similarly, most losses in reintroduced captive-born golden lion tamarins occurred in the first year post-release (Beck et al. 1991) and were due to predation, foraging deficiency and general helplessness in unfamiliar habitat. In fact, feeding errors played a key role, since nearly 20% of the deaths were attributed to starvation or consumption of toxic fruit (Stoinski et al. 2003).

Knowing what to feed on and where to find foods is one of the key skills individuals must acquire. In our study both novice and experienced reintroduced orangutans spent more time feeding than wild conspecifics, but time spent feeding decreased in the experienced compared to novice individuals, as such becoming more similar to wild ones. This change suggests that with experience feeding competence improves. In contrast, other studies did not find differences in feeding time between orangutans with different level of experience and

concluded that reintroduced individuals did not adopt wild-like activity profiles with experience (Grundmann 2006, review: Russon 2009a). However, reintroduction projects on other primates reported changes in activity budgets depending on experience, e.g. in time spent foraging. As such, even though not identical, with experience, activity patterns became similar to these of wild individuals (golden lion tamarins: Stoinski *et al*. 2003, Stoinski and Beck 2004, chimpanzees: Farmer *et al*. 2006). The same pattern of change could be observed in the diet composition.

Wild orangutans spend a majority of their feeding time on fruits (long-term averages range between 52 and 74% across sites: Morrogh-Bernard et al. 2009), which tend to yield higher energy returns per unit time (Knott 1998, Vogel et al. 2015). Our data clearly show an increase in the time spent feeding on fruit in experienced individuals compared to novice. Interestingly, Jambi, who did not survive first year, spent the least amount of time feeding on fruits among the novice individuals. In addition, her overall diet composition differed from both groups of reintroduced individuals (fig s1) suggesting a lack of feeding competence. Study of reintroduced orangutans in Kejeh Sewen also reported an increase in the proportion of fruit consumed by individuals over time (Basalamah et al. 2018).

Since reintroduced orangutans explored significantly more in the feeding context than their wild conspecifics, their diet was more diverse. However, the decrease in frequency of adding new item-species into the diet as well as the decrease in the number of item-species consumed per hour feeding in experienced orangutans compared to novices indicates learning. One could argue that the comparison between Batikap and Tuanan, which are in different habitats, affects this conclusion. However, earlier comparisons showed no differences between lowland forests, such as Batikap, and swamp forest, such as Tuanan, in dietary diversity (Russon et al. 2009b). Second, regardless of how different and diverse the habitats are in terms of number of edible species available throughout the year, the number of item-species consumed in a given hour per day will not reflect that difference. We therefore conclude that the more diverse diet of reintroduced individuals is not just and artifact of the habitat but in fact reflects a lack of knowledge and perhaps also a deliberate strategy: it is often safer to eat smaller quantities of many different foods and so avoid a possibly fatal effect of consuming poisonous food.

In conclusion, we show that necessity drives innovation in reintroduced orangutans, who combined social information with individual exploration to acquire the skills they needed to survive. Over time, they gained experience, as shown by both reduced peering and exploration rates as well as changes in diet composition and size toward the pattern observed

in wild orangutans. Laland and Reader (1999a, 1999b) speculated that necessity may be one of the mechanisms driving animal innovation in line with the saying: 'necessity is the mother of invention'. However, so far there was no evidence for this among wild orangutans. Our results suggest that necessity does indeed make orangutans more exploratory and innovative, although it remains unclear how often such periods would happen under natural conditions and thus what role necessity has played in the evolution of the great intelligence of orangutans (cf. van Schaik et al. 2016).

Although studies of reintroduced individuals in other species show many similarities to orangutans, it is possible that the solitary nature and long life expectancy has made them more conservative and novelty averse than most other species. It is therefore possible that the reports suggesting innovation in response to necessity in wild chimpanzees and its absence in wild orangutans (Yamakoshi and Sugiyama 1995, Gruber 2013) reflect the difference in gregariousness. Experiments indicate less neophobic responses toward novel items in many species when individuals are in the company of others (Forss et al. 2017, Hardus et al 2015). When it comes to food, however, this difference may not be too great, since hungry animals will tend to avoid associations, and solitary chimpanzees and bonobos are even more averse to novelty in captivity than orangutans are (Forss et al. 2019). Alternatively, the extreme conservatism of orangutans was made possible by the phenomenon of community-level mast fruiting in Southeast Asian dry-land forests, which led orangutans to be adapted to long periods of extremely low food availability and thus great knowledge of fallback foods. Thus, when extreme scarcity happened, they would already have adequate responses in place, including physiological ones (Pontzer et al. 2010 – hypometabolism). Regardless, even though the thresholds for unleashing individual-based curiosity may differ, there is evidence that under unusual conditions mature great apes can become curious and exploratory. Paradoxically, the same effect is found when captive orangutans associate with humans and become human-oriented (Damerius et al. 2017a).

These findings may shed some light on the contrast in innovativeness between humans and wild great apes. They allow for two conclusions. One is that at one or more periods our hominin ancestors were faced with serious ecological crises and responded to them with a burst of innovation, despite the risks attached to extensive exploration of novel items. However, because orangutans became less exploratory as they gathered experience and overcame their crisis, this scenario requires that the successful innovators among our ancestors must have had some genetic predisposition to be less neophobic, which was subsequently retained. A second is that humans somehow became like the great apes we can observe in captivity, potentially

because they were encouraged by others, who would reward exploratory individuals with social prestige. At this stage, we cannot distinguish between these two non-exclusive possible explanations for human curiosity (but see van Schaik et al. 2019).

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Chapter 3: The dark side of the red ape: Male-mediated lethal female competition in Bornean orangutans

Anna M. Marzec, Julia A. Kunz, Sonja Falkner, Suci Utami Atmoko, Shauhin E. Alavi, Alysse M. Moldawer, Erin R. Vogel, Caroline Schuppli, Carel P. van Schaik, Maria A. van Noordwijk

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Abstract

Female Bornean orangutans (*Pongo pygmaeus wurmbii)* are mainly solitary and philopatric, leading to adult female relatives sharing adjacent and overlapping home ranges. Females tend to be intolerant of unrelated females, with whom they also may have overlapping home ranges. However, fights that lead to injuries are extremely rare and lethal aggression had never been observed. Here, we report the first case of lethal female-female aggression during over 26,000 hours of focal data collected on adult females at Tuanan, Central Kalimantan: a young female, who had recently lost her infant attacked an old resident female. The interaction's unique feature was that each female received agonistic support from separate, individual males. The attacking female was supported by an unflanged male, who had been in consort with her during the week preceding the attack and was most likely responsible for the lethal injuries to the victim. The victim received support from a flanged male who was probably attracted to the noise generated by the fight. We conclude that even in a species with frequently coercive male-female relationships, female leverage over males can coax males into coalitionary support.

Introduction

Aggression serves ultimately to gain access to limiting resources (Wilson 1975). Although aggression among primates is frequent, lethal attacks are very rare. Young infants are the most likely victims of such attacks in many primate species (Anderson 2000, van Schaik 2000), whereas weaned individuals are far less likely to be a target of lethal aggression. Coalitionary killings of mature conspecifics have been reported so far only in chimpanzees (*Pan troglodytes*: Mitani et al. 2010, Wilson et al. 2014), red colobus (*Procolobus badius:* Strain 1994), capuchin monkeys (*Cebus olivaceus*: Gros-Louis et al. 2003, Mitani et al. 2010), muriquis (*Brachyteles arachnoides*: Talebi et al. 2009) and spider monkeys (*Ateles geoffroyi*; Campbell 2006, Valero et al. 2006). In all these cases, the killing was done by same-sex coalitions.

Female Bornean orangutans (*Pongo pygmaeus wurmbii*) are philopatric while males disperse from their natal range (Morrogh-Bernard et al. 2011, Arora et al 2012, van Noordwijk et al.2012). Female home ranges are relatively small (around 300 ha in Tuanan, Central Kalimantan) and stable over time (Wartmann et al. 2010). Maternally related females tend to have adjacent and overlapping ranges forming social clusters like Sumatran orangutans (*Pongo abelii*: Singleton and van Schaik 2002), but these may also overlap to a similar extent with those of unrelated females (Knott et al. 2008, Knott et al. 2010, Wartmann et al. 2010, van Noordwijk et al. 2012). Related females spend more time in associations and are more tolerant towards each other than to non-related females (van Noordwijk et al. 2012). Between matriline intolerance resulted in a few observed cases of female inflicted non-lethal injuries in Sumatran orangutans (Utami Atmoko: unpublished). Nonetheless, only 6 female-female attacks with physical contact have been observed in Tuanan in 11 years of study, and none of these resulted in visible injuries (current study: unpublished data).

Here we report the first observed female-led lethal attack in a wild population of Bornean orangutans, committed by a female-male coalition. Given the modest intensity of aggression when a female attacks another female independently, the support by the male was probably instrumental in the eventual death of the injured victim.

Methods

The lethal attack took place at Tuanan (2°09’ South, 114°26’ East), which is situated in the Mawas Reserve, Central Kalimantan, Indonesia. The research area consists of 750 ha of peat-swamp forest, previously subjected to commercial selective logging in the 1990’s, and

recovering since then. The orangutans live at a density of approximately 4.5 individuals per square kilometer (van Schaik et al. 2005), which is among the highest in Borneo (Husson et al. 2009). All resident individual orangutans in Tuanan are habituated.

Orangutans are followed during nest-to-nest follows, whenever possible for a maximum of 10 consecutive days, using focal animal sampling following standardized protocols (*cf.* van Schaik 1999, http://www.aim.uzh.ch/research/orangutannetwork/sfm.html). It was not possible to record data blind because our study involved focal animals in the field. Observers are trained and frequently conduct inter-observer reliability tests. This population has been intensively studied since 2003, and most of the individuals, especially the resident females and their offspring have been observed since this time. Their relatedness, social relationships and ranging patterns are already largely known (Arora et al. 2012, van Noordwijk et al. 2012, Ashbury 2013). Until the attack on July 13, 2014, over 26,000 hours of focal data had been collected on adult females.

The participants

Four adult individuals, two females and two males, as well as one immature male were involved in the attacks reported here (Table 1). Kondor, the attacker, is a young female who was known since 2003 when she was estimated to be around 4-5 y old and still nursed by her mother. She gave birth to her first infant in February 2012, but it died 6-9 weeks before the attack. In the 2 weeks before the attack Kondor was regularly seen in association with various flanged and unflanged males. Just before the attack she had been followed for seven consecutive days, during the last five of which she was in a consortship with unflanged male Ekko.

Sidony, the victim, was an adult, resident female ranging in the southeastern part of the study area. To our knowledge, unlike most other females in the study population, Sidony's home range did not overlap with those of adult female maternal relatives. She had at least two daughters; the younger, adolescent one had not yet settled in her own range, while the older one, born around 1997, has not been seen with certainty since early 2006. Despite her advanced age, Sidony had a healthy 4-y old son at the time of the attack. She spent little time in association with her unrelated female neighbors (0.3% of her 768 hours of focal time up to the attack, compared to almost 2% on average for females with related neighbors (see also Fig 1), despite their overlapping home ranges (van Noordwijk et al. 2012). Only two previous encounters between Sidony and Kondor were witnessed, and these occurred when Kondor was still an adolescent.

Ekko has been regularly recorded throughout the study area since 2003, and by 2014 he was larger in body size than all known females and dominant over all other regularly seen unflanged males. Moreover, changes in his facial features as well as behavior suggest that he was in the process of growing flanges (first seen with developed flanges in August 2015) (cf. Dunkel et al. 2013, Marty et al. in press). Over the years, Ekko was often observed in association with resident females, (during 31.5% of 534 hours of focal follow hours on Ekko since 2003), including Sidony.

The final participant, flanged male Guapo, was first seen in the area in 2007, and again in 2012. Since then he was recorded only rarely (on average twice a year). However, Guapo has sired two offspring with females ranging at the periphery of the study area before the start of observations in 2003. Neither Guapo nor Ekko sired any of Sidony's known offspring; and the mature participants in the attack were not related (M. Krützen, pers. comm., see also Arora et al. 2012).

Table 1. Participants of the attack.

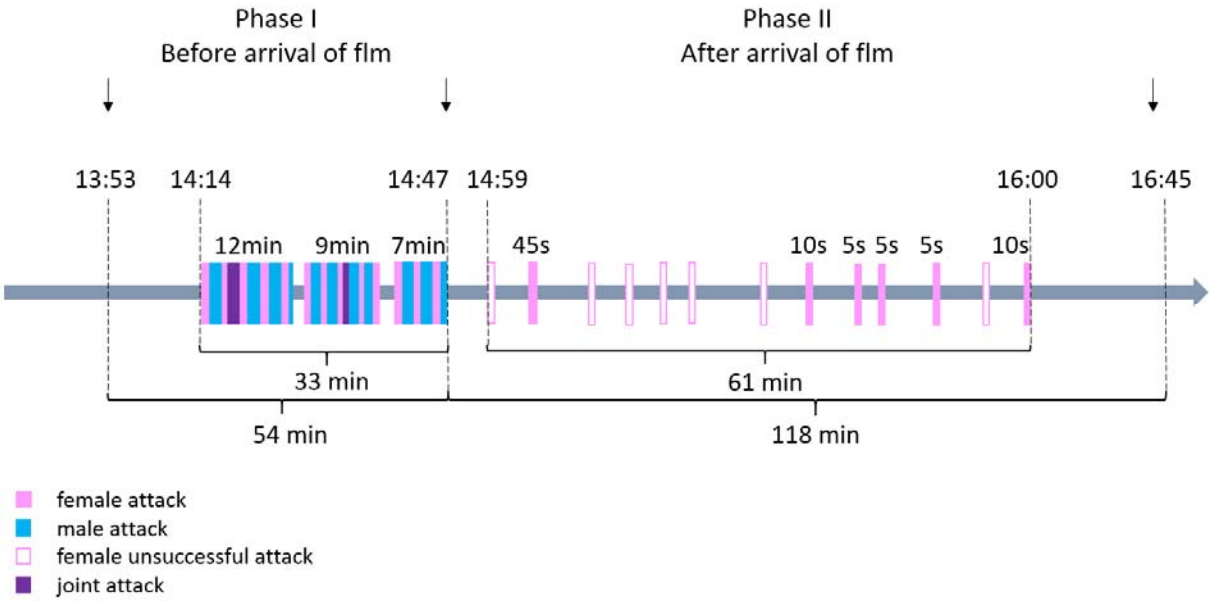
Individual	Class	Age	Known[a] since	Role in the attack
Sidony	adult female with infant	>35	2007	Target of the aggression; suffered fatal injuries; protected her infant and tried to escape multiple times, but did not actively defend herself
Sony	male dependent immature	4.5	born March 2010	Sidony's son; not the target of the attack; not injured; after Guapo arrived also involved in protecting his mother (only against Kondor)
Kondor	young female	c. 15	2003	Main aggressor: initiated, sustained and prolonged the aggression; inflicted a number of injuries
Ekko	unflanged male	>25	2003	Aggressor: supported Kondor; inflicted number of major and life-threatening injuries
Guapo	flanged male	>35	2007	"Defender": protected the victim in active, but non-aggressive way; his intervention kept Ekko at bay and reduced the physical aggression directed at the victim by Kondor

[a] Reliably recognized and subject to focal follows when found

Results

We distinguish two phases of the encounter: before and after the arrival of the flanged male. Figure 1 provides a timeline of the attack (see also Table A in the supplementary material for a detailed description of the encounter).

Fig.1 Diagram of the aggression.



Phase I: Coalitionary attack

During focal follows of both female Kondor and unflanged male Ekko, who were in association, encountered (defined as an approach within 50m) Sidony and Sony in the core area of Sidony's home range. Initially, Kondor and Ekko approached to within 10 m and Sidony did not retreat right away. After about 10 minutes, Ekko sexually inspected Sidony but returned to Kondor to mate with her, whereas Sidony started to move away. Kondor then interrupted her mating with Ekko, approached Sidony and physically attacked her. Immediately Ekko joined Kondor in the attack, which continued for 33 minutes (see Figure 1) with two brief interruptions. During the first fight, Kondor and Ekko took turns attacking Sidony for 12 minutes. When one was involved in physical aggression the other watched and blocked the victim's escape, leaving no more than 45 seconds pause in between. In addition, on two occasions, Kondor and Ekko simultaneously attacked the victim. The attack therefore was coalitionary, continuous and coordinated. Two subsequent attacks took place, lasting 9 and 7 minutes, respectively. All attack sessions were initiated by Kondor, but Ekko inflicted the most serious injuries and was most effective in denying Sidony the chance to escape.

Phase II: Intervention

The dynamics of the fight changed when the flanged male Guapo arrived from likely >100 m away because Ekko retreated from the fight location (>10 but still <50m distance).

Guapo briefly chased Ekko, and mated with Sidony, while Kondor continued to harass her and even bit Sidony in her foot. Whenever Kondor attacked Sidony, Sidony would scream, which prompted Guapo to approach and either move toward Kondor, position himself between them, or move away together with Sidony. Whereas 85% of the attacks were physical in phase I, only 2% were physical in phase II, after Guapo's arrival (Table 2). Moreover, all remaining attacks in phase II were by Kondor alone. Sidony sustained major injuries in phase I but only minor scratches and bites in phase II. This confirms that Ekko caused the most serious injuries and that Guapo was effective in protecting Sidony against additional damaging attacks.

About 45 minutes after the last attack (Fig. 1), Sidony began building a nest, while all other participants were feeding. All individuals made a nest within 50m of each other, with Guapo in between Sidony and Kondor whereas Ekko's nest was farther away.

Table 2. Result of flanged male intervention.

	Before intervention	After intervention
Duration of aggression	33 min	61 min
Total time of physical aggression	28 min	1min 20s
Aggressors	Ekko, Kondor	Kondor
Type of attack	continuous, coordinated and coalitionary	brief, single attacks
Type of injuries	serious wounds resulting from bites on arms and legs; bites and scratches on the back and head	minor bite wounds on hands and feet
Prevented and interrupted attacks	None	All
Unsuccessful attacks	None	Many

Subsequent events

On the morning of day 2, Kondor left her nest and immediately approached Sidony, but Guapo intervened instantly and mated with the victim. Ekko left the association in the morning. Kondor kept trying to attack Sidony but Guapo intervened every time and interrupted physical contact between the females. Kondor left Sidony (>50m) at the end of the day and was followed by Guapo. Both Sidony and Sony frequently groomed and licked her wounds.

On day 3, Kondor came back to Sidony twice and tried to attack, but Guapo followed Kondor and intervened. All of his interventions were non-aggressive, as on previous occasions. Kondor eventually left, followed by Guapo. Guapo was not observed to mate with Kondor that or any other day following the attack.

On day 5, Ekko came back alone to the location of the attack, where Sidony was still present, since she had not moved. Ekko did not attack her. On day 6, Ekko revisited the location of the attack again and watched Sidony for 30 minutes from the distance of 15m. He did not approach her nor was he aggressive towards her.

On day 10, Sidony's offspring Sony left and nested alone over 100m away from his mother and did not approach within 50m for the subsequent days. Sidony was last seen alive on day 12. She was found dead on the ground on day 16. The stage of decomposition suggested she died one or at most two days before she was found, about two weeks after the attack.

Sidony's infant Sony has been seen since the attack, and was observed in March and April 2015 in association with his adolescent sister, indicating he had survived without his mother. He was around 4.5 years old at the time of her death and not yet weaned, whereas so far the youngest known immature to be completely weaned in Tuanan was 5.5-6 years (van Noordwijk et al. 2013). Kondor has frequently been seen throughout the study area since the attack. She showed clear sign of pregnancy (and a human pregnancy test was positive) in November 2014, and gave birth in late March/early April 2015. Therefore, she conceived around the time of attack or shortly afterwards, and within only 2 – 3 months after losing her first offspring.

Discussion

Lethal aggression among primates is rare. Individual attacks that turn lethal are most likely in territorial species (Palombit 1993), but orangutans are not territorial, and aggression among males is far more likely to escalate than that among females (unpublished data) and is known to lead to facial scars, missing fingers and toes and even death (Knott 1998, Dunkel et al. 2013). The lethal cases in group-living species are exclusively based on coalitionary aggression by same-sex coalitions, and often in the contexts of attempted takeovers or between-group conflicts: chimpanzees (Wilson et al. 2014), spider monkeys (Valero et al. 2006), and capuchin monkeys (Miller 1998, Gros-Louis et al. 2003), and red colobus (Starin 1994).

The orangutan case reported here does not comfortably fit that pattern. It was coalitionary, but it involved between-sex coalitions. This is quite unexpected, as in wild orangutan males and females have never been reported to form coalitions before. Although captive studies report male interventions in female conflicts, these were peaceful and tended to terminate aggression (Edwards and Snowdon 1980, Zucker 1987), whereas in another study the interventions in female-female agonism were by female or a juvenile male (Tajima and Kurotori

2010). Nonetheless, because females attacking alone are not known to severely injure other females, the explanation for the lethal outcome of the attack should be sought in its coalitionary mixed-sex nature.

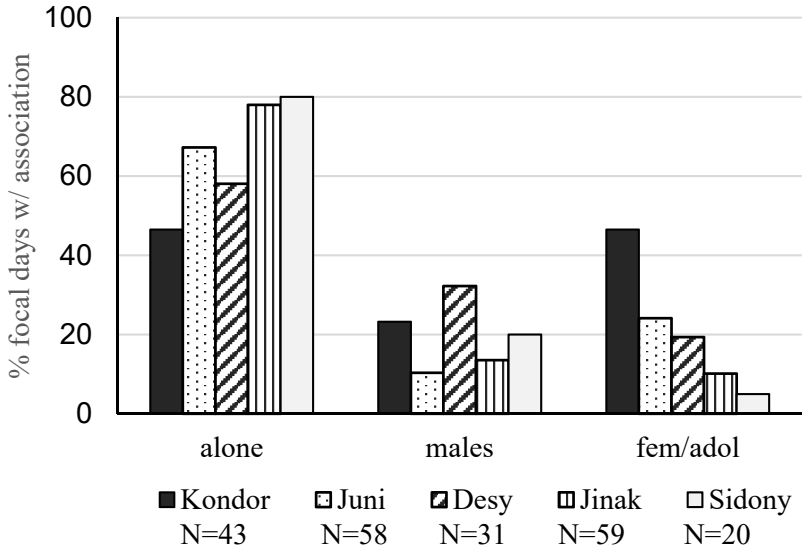
Fundamentally, the observed polyadic interaction reported here is an expression of female-female competition as the aggression was initiated, prolonged and maintained by Kondor against Sidony. Indeed, Kondor continued with physical harassment even after the departure of her coalition partner, while her partner, Ekko, was not aggressive towards Sidony few days after the attack, once Kondor was no longer present.

Previous observations at Tuanan showed that female-female competition over range use is intense. Although adult female Bornean orangutans are not territorial, they do establish overlapping home ranges, where mothers spend much of their time alone and only in the company of their own (semi-) dependent offspring. In 2002-2003 an adult female (Sumi) with dependent offspring (Susi) lost her habitat due to logging, mining and fires. Over a period of several years she shifted her range into study area where she had no maternal relatives (Arora et al. 2012). Sumi avoided close encounters by remaining very quiet, and upon discovery descended to the ground and moved away as inconspicuously as possible (cf. Ashbury et al. in press). Even though the resident females chased her whenever they discovered her, physical fights were never observed and she eventually died in August 2006 as the result of the attack by a clouded leopard (unpublished data).

In the current case, the female-female interaction escalated between two residents in different phases of their lives, one old and one early in her reproductive career. Kondor, a young member of the largest local matriline, had recently lost her first infant. In general, adolescent females start to explore beyond their natal home range but settle where they least encountered other females, including their own mother, before the birth of their first offspring (Ashbury 2013). However, after the birth of her first infant, Kondor still ranged over a larger area than all other known females in similar reproductive state (unpublished data). In addition, compared to other mothers with offspring under 3 years old during the same period (July 2010-July 2014), Kondor spent fewer days alone and she associated on many more days with other females and adolescents (Figure 2). However, Kondor's high association rate was not due to more frequent social play with associates by Kondor and/or her offspring compared to other mother-offspring dyads (Kunz 2015), even though social play is the major positive social interaction during associations of orangutan mother-offspring dyads (van Noordwijk et al. 2012). On the other hand, there is no evidence that Kondor was more often agonistically displaced by other females.

Nevertheless, the high encounter frequency does suggest, Kondor was experiencing increased pressure from the other resident females and adolescents (mostly her known relatives).

Fig.2 Comparison of the percentage of nest-to-nest follow days that a female with 0-3 y old infant was not in association with any other independently traveling individual, with a male (unflanged or flanged) or with another female (with or without offspring) or adolescent. Females are in order of known parity: Kondor with 1 infant (died), Desy and Juni with 2, and Jinak and Sidony with more. Note that on the same day a female can be in association with males and females.



Infant mortality in wild orangutans is reported to be much lower than in other great apes (Wich et al. 2009). In the Tuanan population, Kondor's infant is the first to have died in 1084 infant observation months (including all pre-weaned known offspring) or a rate of 0.011 deaths / infant-year. Even though the circumstances of the loss of her infant remain unclear (it seemed healthy at last sighting), it is likely that Kondor's particular condition contributed to her unusual, aggressive behavior. Her consortship with a long-known partner may have contributed to her confidence to fiercely attack the female she had occasionally encountered before and was chased and hit by on at least one occasion when Kondor had just started to roam without her mother in 2009.

Without the involvement of Ekko, it is unlikely that Sidony would have incurred such severe wounds, and the fight would probably have ended within the first 7 minutes (see table A Supplement), during one of the breaks in which Sidony started to move away. Ekko's active participation in the attack on Sidony can be interpreted as his investment in the consortship with Kondor. It should be noted that at no time did Ekko attempt to copulate with the victim (he had

inspected her briefly before the attack and shown no further interest), and his injuring Sidony can therefore not be interpreted as extreme force during a forced mating attempt. The observation that Ekko did not attack or try to mate with Sidony a few days later when he was on his own supports this argument. Thus, Ekko's participation in the lethal aggression was not due to a mating conflict with Sidony but instead elicited by the presence and actions of the consorted female.

Ekko and Kondor were ranging together for five days before the attack. It is likely that to maintain this association and to increase his chances to sire Kondor's next offspring, which was conceived around that time, Ekko supported her during the attack. Benefits from maintaining a tolerant association with a female may include more cooperative mating opportunities, in contrast to coerced matings more often seen during short associations (Dunkel et al. 2013). Therefore, Ekko's behavior can be explained as his investment in maintaining the association with Kondor. By supporting her and showing his fighting abilities he could influence her choice to willingly maintain her consortship with him.

Young females are known to use sexual proceptivity as a 'sexual passport' (e.g. Goodall 1986). By attracting males and associating with them, a young female gains safety to move throughout an area outside her natal range without being at risk of potential aggression from unfamiliar resident females (Ashbury 2013).

In the attack reported here Guapo intervened in the conflict and separated aggressors and victim multiple times over a period of three days. Guapo's intervention included threatening the unflanged male, approaching the aggressor, positioning himself between the two females and "guarding" the victim. None of the actions against Kondor involved aggression on his part, but each either terminated the aggression or prevented physical contact between her and Sidony. A male's interest in securing his access to multiple females may explain Guapo's effort in protecting one female without attacking the other. Nevertheless, perhaps surprisingly, Guapo was not seen to mate with Kondor during or after the attack, nor did he remain in consortship with her after Ekko and Kondor left Sidony together on the third day.

Conclusion

Male-female coalitions have not been described for wild orangutans, and must therefore be extremely rare. The most plausible interpretation of the lethal attack here is that males in consort with a female must not only show great tolerance, as when females take food from them (van Noordwijk and van Schaik 2009), but can also be recruited to support them in their

competition with other females, including participation in attacks. This suggests that fertile females have great leverage (Lewis 2002) over males, if only because they can end the association by attracting other males. This is remarkable because of the huge sexual dimorphism and high potential for sexual coercion in orangutans, as reflected by the high proportion of matings that are forced (Fox 2002), especially on Borneo (Knott et al. 2010).

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Chapter 4: Within-population variation in nest building behaviors of Bornean orangutans (*Pongo pygmaeus wurmbii*): individual plasticity and cultural influences

Anna M. Marzec, Piero Amodio, Alison M. Ashbury, Sri Suci Utami Atmoko, Maria A. van Noordwijk, Carel P. van Schaik

Abstract

Orangutans spend the night in arboreal nests they construct each day. Complex object manipulation and cognitive flexibility is needed to build elevated stable platforms given great variation in within-tree site architecture and the wood properties of each tree species. In addition, nests can be enriched with elements that increase comfort, such as pillows, blankets and/or roofs. Moreover, an individual's nest building repertoire may include nest-specific vocalizations, twig biting and smoothing, as well as carrying in nest material from outside the nest tree. Since orangutans acquire their nest-building skills through the peering-practice cycle, mainly from their mothers, we can expect cultural variation in nest building techniques. Local traditions, such as nests built on multiple trees, have been described before. Here, we investigated the variation in nest building within a single population of Bornean orangutans (*Pongo pygmaeus wurmbii*). We used data on a total of 6427 nesting events observed during focal follows of mature individuals at Tuanan, in Central Kalimantan, and 200 deconstructed nests. The long-term data enable us to create behavioral profiles of individuals' nesting habits, and relate dyadic similarities to genetic relatedness, social exposure, and home range overlap. Our results showed no significant differences in nest position, species choice and building techniques between residents (females) and immigrants (males). We also found no differences among different female mtDNA haplotypes, reflecting clusters of social contact, apart from some variation in nest tree species selection and leaf carrying. In conclusion, we demonstrate that orangutans show rich individual flexibility in nesting behavior and found no effect of social barriers on the spread of behavioral innovations related to nest building, suggesting the cultural unit for nest-building extends well beyond the study area.

Introduction

Nests built by great apes are bed-like sleeping platforms assembled from branches and leaves. Unlike the nests built by other taxa as breeding sites or shelters (Hediger 1977, Kappeler 1998), ape nests are constructed daily and their main function is to provide comfortable resting sites (Anderson, 2000, Stewart et al., 2007). In addition, nests can serve as protection from predation, parasites such as mosquitos, and help with thermoregulation (Fruth and Hohmann 1996, McGrew 2004, Koops et al. 2012). Most great apes, except for gorillas, tend to build arboreal structures rather than ground nests (Fruth and Hohmann 1996).

The ability to build stable elevated sleeping platforms is learned skill that requires both early exposure to skilled role models and experience achieved through extensive individual practice (Bernstein 1962, Goodall 1986, Fruth and Hohmann 1994, Videan 2006, Schuppli et al. 2016a). Moreover, it also requires high technical and cognitive skills compared for instance to those needed for tool use (McGrew 1992, Hansell and Ruxton 2007). Complex object-manipulation skills are necessary in order to quickly create comfortable and well-supported arboreal sleeping platform using surrounding branches. In addition, cognitive flexibility is required to build nests in spite of enormous variability in within-tree site architecture and in wood properties (toughness, flexibility) of each tree species (van Casteren et al. 2012).

Of all apes, the nests built by orangutans are considered the most complex and elaborate (Groves and Pi 1985, Ancrenaz et al. 2004). Nest building involves a number of actions such as choice of the nest tree(s) species, choice of nest position within the tree, collection of materials, and the actual construction of the nest (Russon et al 2006, Prasetyo et al. 2009). The basic platform may be enriched with additional comfort elements, such as a pillow, a blanket and a roof. This great variety of skilled behaviors (van Casteren et al. 2012) provides great potential for innovation, which once spread and retained in a population, can become cultural.

In fact, many of the cultural variants already described in orangutans are found in the nesting context. These are present (habitual and/or customary) in some but absent in other populations without ecological or genetic factors explaining this variation across sites (van Schaik et al. 2003, 2006, Russon et al. 2009, van Schaik et al. 2009, Bastian et al. 2012). Immature orangutans peer (i.e. intently observed from a close distance) at all activities of their mothers and others that are novel and/or complex, and practice the peered-at activities until they have basically acquired their mother's behavioral repertoire by weaning (Jaeggi et al 2010, Schuppli et al. 2016a, Schuppli et al. 2016b). As expected based on its complexity, nest-building behavior is intensely peered at (the second-most frequent target of peering after

feeding: Schuppli et al. 2016a), already beginning at age 6 months. This strong social influence suggests the potential for cultural transmission of nesting behaviors and nest building techniques.

Peering is almost always followed by extensive practice. By age 3y infants are capable of making small and stable sleeping platforms (van Noordwijk and van Schaik 2005) that serve mostly for play purposes and a short resting session during the day (pers. obs.). The number of built practice nests then gradually decreases (Schuppli et al. 2016a) and the nights are still spent in mother's nest. Sleeping in mother's nests may also serve as a source of knowledge: using a nest built by a skilled nest builder allows the immature to experience both qualities and properties of different constructions of sleeping platforms built on variety of tree species. When the younger sibling is born, the mother often refuses to allow the older offspring in her nest and the immature has to sleep in its own nest. By then they are very capable of building stable sleeping platforms, although they presumably still benefit from mother's knowledge and choice of sleeping site because they often nest in the same tree (pers. obs.). This long time until immatures achieve full independence in building their own sleeping platforms shows the complexity of both choices and actions.

Since among Bornean orangutans, adults spend little time in association with each other, the opportunities for learning decrease dramatically upon reaching independence, apart from a period of increased association with peers during adolescence (e.g. Galdikas 1985). Thus, as in the case of other behaviors, their set of nest-building skills is expected to resemble that of their mother. However, we can make some predictions about the presence of possible cultural units. First, the predominantly vertical social transmission (i.e. from mother to offspring) of nesting behaviors, combined with female philopatry and male dispersal (Arora et al. 2012), could lead to differences in nesting repertoires between resident females and immigrant males, which may come from far away (Nietlisbach et al. 2012). Second, at a finer level, both the presence of clusters of related females and the females' preference for associating with same-sex maternal relatives (van Noordwijk et al. 2012, Ashbury et al. under review) suggest the existence of social barriers (Marzec et al. 2016) within local populations, which could limit social transmission of nest-related techniques, tree choice and innovations. Therefore, we may expect differences in nesting skill sets and tree choice between maternally related females and maternally unrelated ones.

On the other hand, there may be reasons to expect little within-population variation in nest building. First, the long period of practice may equip individuals with experience and motor skills that they acquire independently from social influences. Second, besides social learning

through direct observation of the nest building process, they can acquire some information about nest construction by examining already built nests. Nests with the entire set of elements intact are known to be sturdy and last on average, for about a month (Morrogh-Bernard et al. 2003, Johnson et al. 2005, van Schaik et al. 2005, Mathewson et al. 2008), and much longer than nests of other apes (Groves and Pi 1985, Ancrenaz et al. 2004). Thus 'old nests' are likely to be a source of information on tree species and nest position choice as well as techniques and elements used. As a nest decays, leaves fall off showing how the branches were tied together and how the nest is situated in the tree. Orangutans roaming through the canopy often encounter nests built by conspecifics, and occasionally also reuse and rebuild them, thus directly interacting with nests built by other individuals (Prasetyo et al. 2009, pers. obs.), which provides additional learning opportunities. Therefore, acquisition of nest-related variants might depend less on only close-range direct observation of the activity compared to, for instance, acquisition of the diet and food processing skills (cf. Bastian et al. 2010). At the same time, both motivation and attention to learn and expand their own nest building repertoire after weaning might be lower than in the feeding context. Thus, even though we expect differences in nest building techniques and tree choice between males and females as well as different female matrilines, these additional opportunities for the spread of nesting techniques and innovation across entire population might make the differences linked to social barriers less pronounced.

Orangutan nests have been studied mainly to estimate population densities (van Schaik et al. 1995, Buij et al. 2003, Felton et al. 2003, Wich et al. 2004, Johnson et al. 2005, van Schaik et al. 2005, Husson et al. 2009). However, some studies focused on investigating nest-building behaviors (Sugardjito 1983, Ancrenaz et al. 2004, Russon et al. 2007, Wich et al. 2009), which led to identifying several nest-related cultural variants (van Schaik et al. 2003, 2006, 2009). Here, we use long-term data on nest building behaviors and detailed data of deconstructed nests from identified mature individuals of the wild, well-studied orangutan population in Tuanan, Central Kalimantan, to investigate patterns of within-population variation in nest building techniques and nest tree choice. We compare resident individuals (females) with migrants (males) as well as females with different mtDNA haplotypes in order to explore within-population variation in nest-building techniques and choice of nest tree species and evaluate the patterns in this variation and whether these patterns are cultural. The results of this study contribute to identifying cultural units in orangutans.

Methods

The data on nest building behavior were collected using a standardized protocol (cf. van Schaik 1999, http://www.aim.uzh.ch/research/orangutannetwork/sfm.html) during focal follows between 2003 and 2018. The additional, detailed data on nest building techniques were collected between 2013 and 2015 during manual deconstruction of the nests.

Study site and population

This study was conducted on the wild Bornean orangutans (*Pongo pygmaeus wurmbii*) in Tuanan Orangutan Research Project (2°15′ S, 114°44′ E), located within the Mawas reserve in Central Kalimantan, Indonesia. The individuals of this population have been continuously studied since 2003, are individually recognized and their ranging patterns as well as social and genetic relationships are largely known (Arora et al. 2012, van Noordwijk et al. 2012): All females (7) with haplotype B were closely related, the 2 haplotype C females were a mother-daughter dyad, whereas there was only one known mother daughter-dyad among the 6 females with haplotype A (see fig. 13). The Tuanan orangutan population has one of the highest densities on Borneo (Husson et al. 2009) of 4.5 ind/km^2 (van Schaik et al. 2005), with females having relatively small, but highly overlapping home ranges (Wartmann et al. 2010, van Noordwijk et al. 2012, Ashbury et al. under review). The study population inhabits peat-swamp forest selectively logged 25-30 years ago.

Data collection

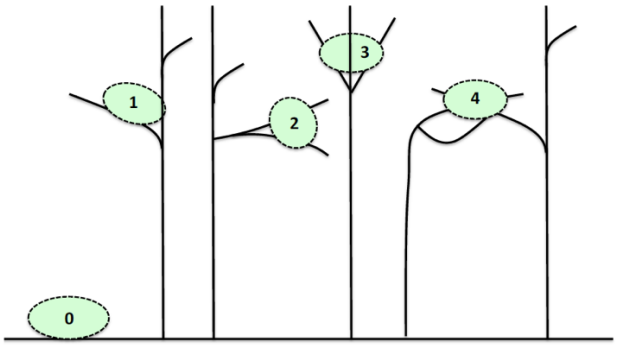
The general data on nest building behaviors and on nest tree choice were recorded during focal follows whenever the followed individual built a new nest and rebuilt or reused an already existing one. The following information about nesting tree(s) was collected: number of nest trees involved, their species, height, and diameter at 1.2m height from the ground (dbh). The details recorded of the nest included: nest position (see fig.1), nest height estimate (in 5m classes), presence of additional elements such as pillow, blanket, roof, and type and number of nesting vocalizations. In addition, we also noted the presence or absence of known cultural variants such as twig biting, smoothing twig ends with the mouth, and the collecting and carrying of nesting material from outside of the nesting location (known as ‘leaf carrying’). In the case of leaf carrying, additional details were recorded, including tree or liana species, time

of collection (before start of construction, during, or after nest was built) and distance over which the material was carried.

In total, we observed 6427 nests being built by mature individuals. We provide a general overview of the nest data set and nest-building habits of Tuanan orangutans in the supplementary material (table s1 and s2). For the analysis, we used data collected by selected well-trained observers with high inter-observer reliability scores, recorded during daytime and under good visibility and weather conditions. In addition, only new, arboreal night nests built by individually identified mature individuals for which we had minimum of 10 nests observed were included in the final sample (leaving N= 3750).

Detailed data on nest architecture were collected by manually deconstructing the nests (N=200) within less than two weeks since they were built. Four observers, all trained in tree climbing, measured and deconstructed nests and recorded the entire process using GoPro camera. Video recordings were coded by AM (60%) and PA (40%), who also deconstructed majority of the nests (44% and 40%, respectively) and had very high inter-observer reliability score (Kappa = 0.95 based on 20 videos scored by both). For the analysis we only used new night nests built by identified, mature individuals for which at least 5 nests were deconstructed (N=164). The data collected during deconstruction included information on nesting tree(s), namely its species, height, dbh and tree architecture (classified in one of 6 types based on Halle and Oldeman 1970, see fig. s1), and about the nest itself, namely its height, length, width, depth and nest coverage (i.e. 0, 25, 50 and 100%). During the deconstruction process, we scored the presence and type of each construction element: foundation, platform, rim, lining, pillow, blanket and roof (table 1, fig.2). We also recorded the presence of other plant species than those directly supporting the nest. Finally, we counted all loose branches found in the tree canopy and on the ground below the nest that were used as blankets and had fallen out of the nest when the individual left the nest in the morning.

Fig.1 Nest positions: 0 – nest built on the ground, 1-3 nest built in different locations within a single tree, 4 – nest built using more than one tree.



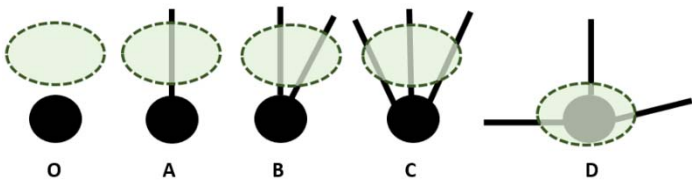
Since all deconstructed nests were built by focal individuals, we could also use them to check the accuracy of the direct behavioral observations. This is necessary because orangutan nests are often built high in the forest canopy and usually in the late afternoon, so observers cannot always see and record all the details of the nest construction process. Overall, the information on the most obvious features of the nest such as nest position, nest tree species and number of trees used for nest building was highly reliable (table s3). The same was true for most information on presence or absence of the additional elements and occurrence of leaf carrying. The one exception was pillows, which had surprisingly low reliability score. In 50% (N=6) of the cases no pillow building was noted at the time of nest building while the pillows were found in deconstructed nests. It is possible that in these cases pillows were added to the nest after observers finished data collection and left. In the other half of the cases where the mismatch was reversed, it is possible that loose branches added to the nest, which observers had identified as pillows, were in fact the lining. The sample sizes for additional elements and leaf carrying varied due to missing data (i.e. scored as "unknown" due to poor visibility at the time of data collection) (see table s3 and fig. s2 for details). Obviously, other cultural variants such as twig biting or twig end smoothing with mouth also could not be assessed during the deconstruction. Based on this reliability analysis, we decided to use the big behavioral data set for analysis of nest position and tree species choice, and to rely on deconstructed nests for the analysis of nest architecture. Effective sample sizes used in the analysis are provided in table s4.

Table 1. Definition and function of nest construction elements.

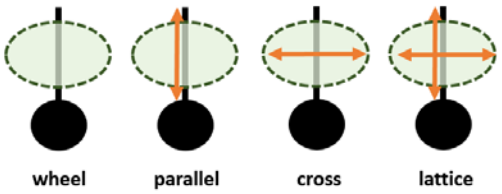
Element	Description	Function	Scored
Foundation	A stable, pre-existing surface of one or more branches that are supporting the nest. It is selected prior to the start of the construction of other nest elements.	Structure	5 models (fig 2a)
Platform	A basic structure of the nest. Built by breaking, bending and tucking in branches toward the center of the nest.	Structure	4 models (fig 2b)
Rim	Curved branches around the platform, wedged into a form of a circular edge.	Structure	Presence or absence
Lining	A collection of detached leafy twigs and branches placed on the bottom of the nest and distributed evenly. It is constructed to increase comfort of the nest.	Comfort	Presence or absence
Pillow	Short detached leafy twigs piled up in one location of the nest and arranged in one of the four ways. It is used to increase comfort of the nest.	Comfort	4 models (fig 2c)
Blanket	Detached leafy twigs and branches used to cover the body	Comfort	Presence or absence
Roof	A separate structure (sometimes nest-like) built from attached and bent branches above the nest, creating protection from rain	Comfort	Presence or absence

Fig.2 Models of nest construction elements, as viewed from above: a) foundation, b) platform and c) pillow.

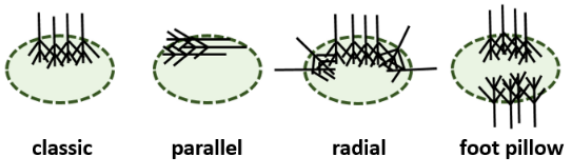
a) Foundation:



b) Platform:



c) Pillow:



In addition, we collected data on tree species abundance and tree architecture using two kinds of plots. Data from the three phenology plots covering a total area of 2ha with 1604 trees of dbh ≥10cm identified to 85 species were used to calculate tree availability. Furthermore, we collected data on tree architecture of all trees within nest plots (5m radius from main tree of deconstructed nests). We only used data from non-overlapping plots spread throughout the study area and for trees bigger than the smallest nesting tree (dbh and height) resulting in 1939 trees identified to 84 species.

Analyses

We tested two predictions 1) that resident individuals i.e. females differ in their nest tree choice and nesting behaviors from males, who are all immigrants and 2) that maternally related females differ from maternally unrelated females. At Tuanan, we find various mtDNA haplotypes close in space, suggesting that females belonging to the same haplotype share a rather recent common ancestor and are thus show above-average relatedness and associations. See table s5 for sample size for each compared group.

First we visualized the data and whenever there was a visible effect we used ANOVA to formally compare groups. When the effect was found the Tukey HSD post-hoc test was used for comparisons between specific groups. Whenever we used multiple testing, Bonferroni correction was applied. In addition, we used Jacob's index (Jacobs 1974) to evaluate whether nest-tree selection such as choice of species and tree architecture are based on availability of particular trees. For nests built on multiple trees we only considered the main tree due to its overall contribution to the nest construction as well as the fact that primary choice was directed towards selection of the single tree (pers. obs). Further, we used Chi-square statistics to assess if there was an overall preference for either tree species choice or the tree architecture. Significance was assessed by building Bonferroni confidence intervals (Neu et al. 1974). All analyses were performed in R (version 3.4.3). In addition, we used binomial generalized linear mixed effect model with individuals as intercept for analysis of the data containing multiple observation per individual using the lme4 package (Bates et al. 2014).

Results

First we visualized tree species choice and nest positions built by Tuanan orangutans, and compared (a) females with males (unflanged and flanged), and (b) the three main female haplotypes.

Tree species choice

Overall, 97 tree species were used as a main tree in all 3750 nests (table s6). For all the nests built on multiple tree nests we only included the main nesting tree. Interestingly, the majority of nests (55%) were built on just 7 tree species (fig. 3). Among remaining 90 species, only 28 accounted for >1% while the rest was below that threshold. Thus, for the analysis we used 7 most used species, each accounting for at least >3% of all nests. For each individual, we calculated the proportion of nests built on the most used tree species. The selection of tree species used by females, unflanged and flanged males were very similar (fig. 4a). Visual inspection of data showed that there were no noticeable differences: females and both male morphs most frequently used the same species *Elaeocarpus mastersii*. More variation was detected among female haplotypes. In particular, there was a difference between the three haplotype groups ($F(2,12)=4.33$, $p=0.038$) in the use of *Campnosperma coriaceum* (fig. 4b). For females from haplotype A, this species was the most frequently used tree, while females from haplotype C hardly ever used it. In fact, out of 223 nests built by haplotype C females, a

mother-daughter pair, only 4 were built on a single *Campnosperma coriaceum* tree and this species was never included in a multiple-tree nest (n=94). Although the overall difference among 3 haplotypes for use of this species in nests was significant, pairwise comparison with Tukey post-hoc test showed only a trend for a difference in use between females of haplotype B and A (adjusted p=0.059) and no significant difference between haplotypes C-A as well as C-B (adjusted p=0.099 and p=0.859 respectively).

Fig.3 Proportions of the top 7 tree species used in ≥50% of night nests built by Tuanan orangutans (N=3750).

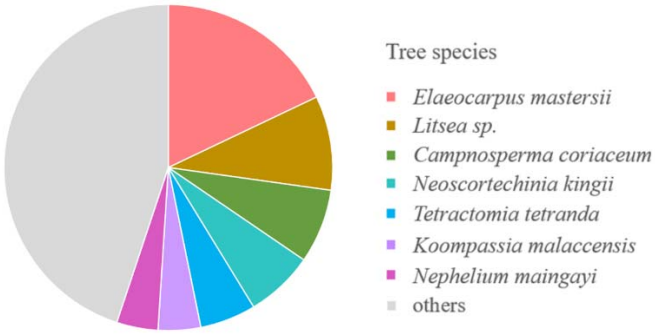
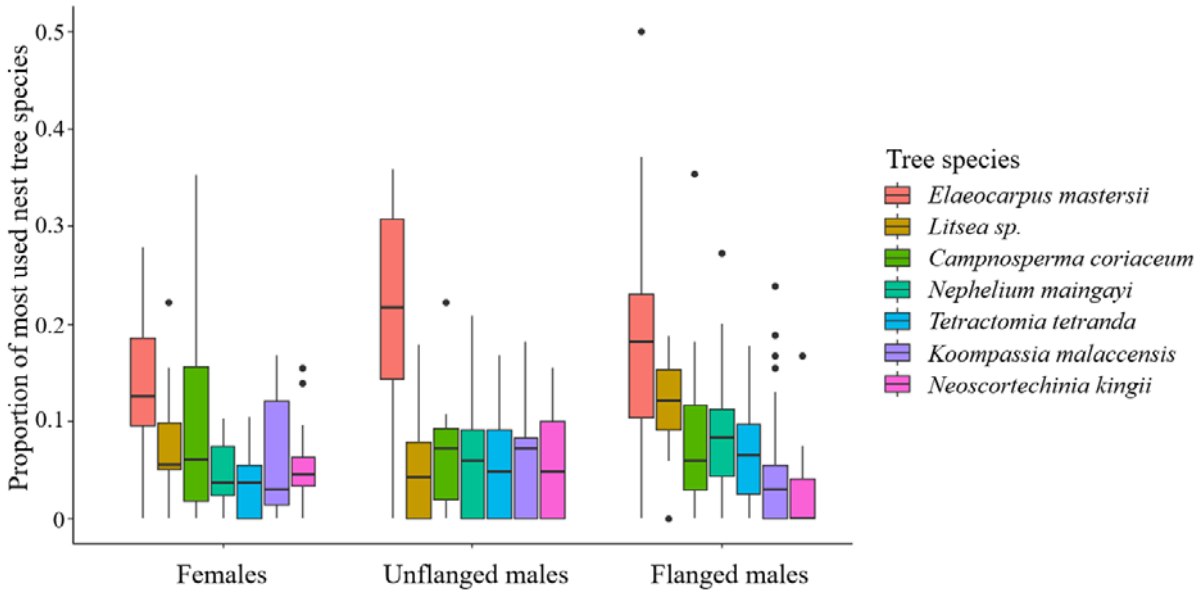
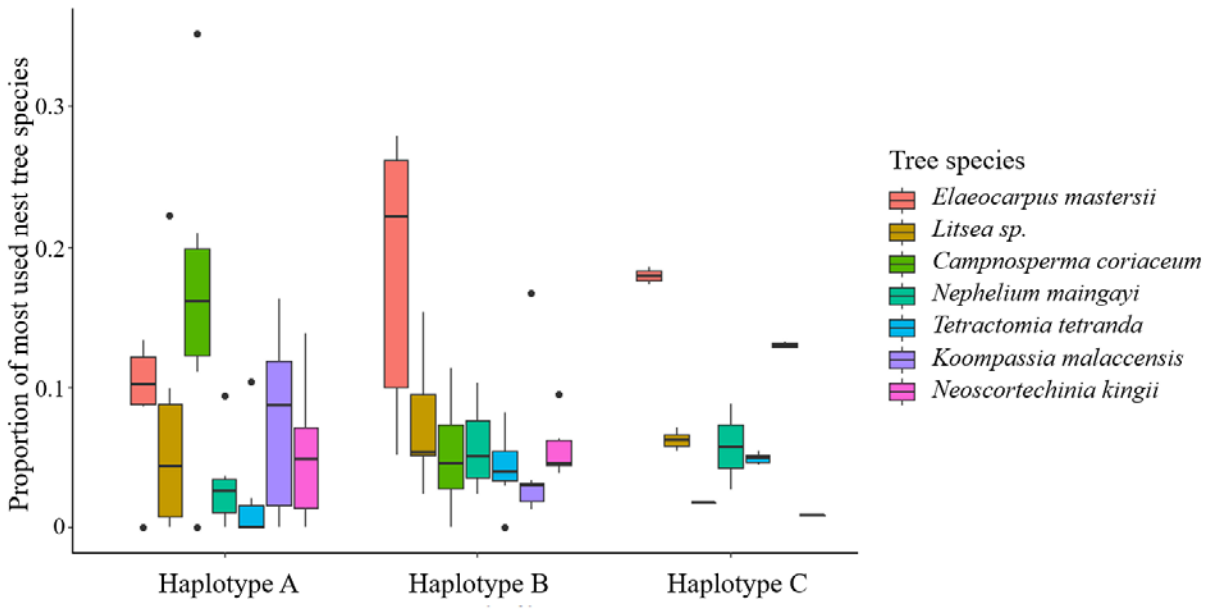


Fig.4 Proportions of the seven most used nest tree species by each individual, grouped (a) by sex, with males divided into unflanged and flanged morphs, and (b) by female haplotypes, based on data collected during focal follows (N=3750).

a)



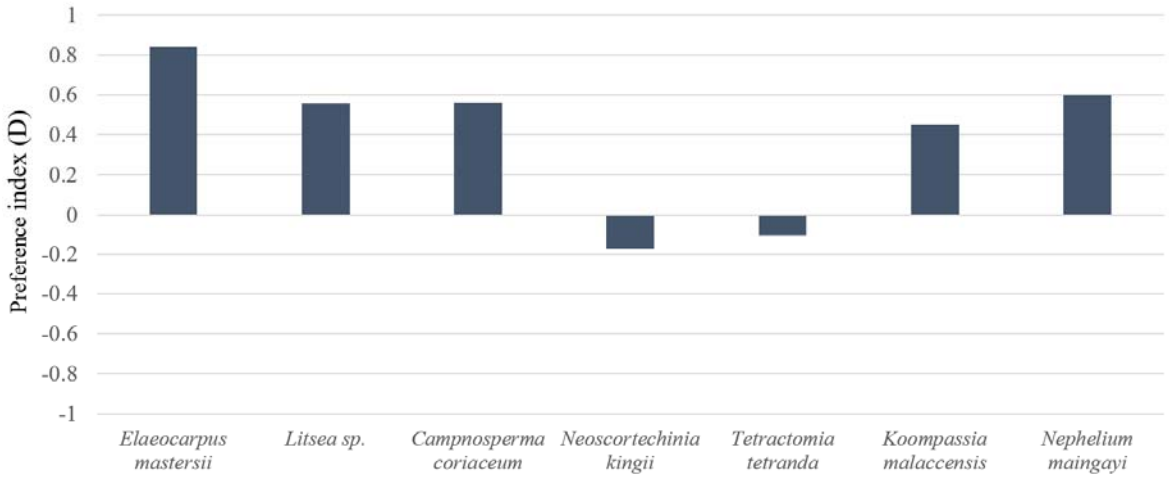
b)



In order to evaluate whether the nest tree choice reflects the preference of particular species or simply its availability in the habitat, we used data from tree phenology plots (see methods) to calculate Jacob's preference index (D). Five out of seven top nest species were clearly used more than available ($D \geq 0.5$, fig. 5). In particular, *Elaeocarpus mastersii*, most used nesting species, was actively selected (D=0.8) compared to its availability in the habitat. The two species with negative values, yet close to zero, reflect nearly proportional use of these species. In fact, *Neoscortechinia kingii* and *Tetractomia tetranda* were the first and third most common tree species recorded in the phenology plots respectively. However, there were no significant overall preferences ($\chi^2_{(7)} = 1.91$, $p = 0.965$).

Next we checked whether tree architecture influenced the choice of the nesting tree using Jacob's index. None of the architecture types were chosen more than expected based on availability (D>0.5) and there was no significant overall preference ($\chi^2_{(6)} = 0.135$, $p = 1$) for any of them. No nests were built in the type 3 trees (fig. s3), but due to its overall low availability in the habitat (4%, see fig. s4) we cannot conclude that this tree type was actively avoided. It should be noted that individual trees of each of the top 7 nesting tree species showed many different architecture types (fig. s5).

Fig.5 Jacob's preference index for the top seven nest tree species used by Tuanan orangutans, where -1 = indicates total avoidance; +1= indicates preferential use and 0 = proportional use.

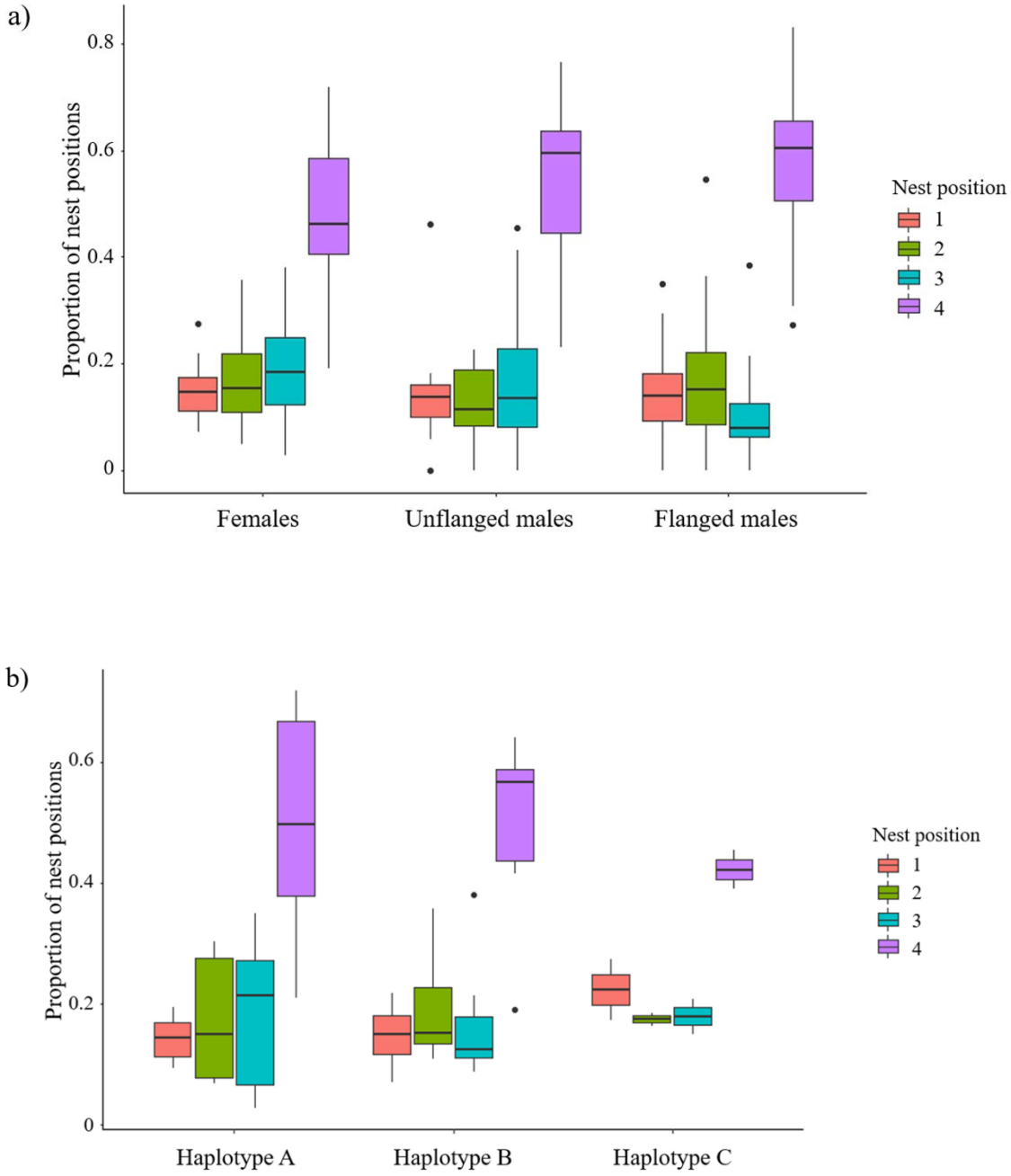


Nest position

In Tuanan, more than half of all nests (56%) were position 4 nests, while the other positions (1, 2 and 3) were much less frequent (fig. s6). Visual comparison of nest positions built by females, unflanged and flanged males did not reveal any differences between the nests built by either of these classes (fig. 6a, see also table s7). Similarly, no noticeable differences were found among different female haplotypes (fig. 6b, table s8). Indeed, within each sex-age class, position 4 nests were built more often than any other position and the same was true for the female haplotype groups. At the individual level, all orangutans regardless of their sex or genetic relatedness built all nest positions. Most of them built position 4 nests more often than any other nest position (fig. s7).

Another way to look at nest construction, rather than its position within a tree, is to consider how many trees were used to construct the nest. Only position 4 nests involve multiple trees (see fig.1). In Tuanan, less than half of the nests (44%) were built on a single tree (fig. s8). The proportion of nests in single and multiple trees was very even within both sexes (fig. s9a) and there was no significance difference between the females, unflanged and flanged males ($F(2,54)=2.29$, $p=0.11$). Among females only haplotype C females built more single tree nests (fig. s9b), but differences among the female haplotypes were not significant ($F(2,12)=0.16$, $p=0.85$).

Fig.6 Proportion of nest positions built by each individual, grouped (a) by sex, with males divided into unflanged and flanged morphs, and (b) by female haplotypes. based on data collected during focal follows (N=3750).



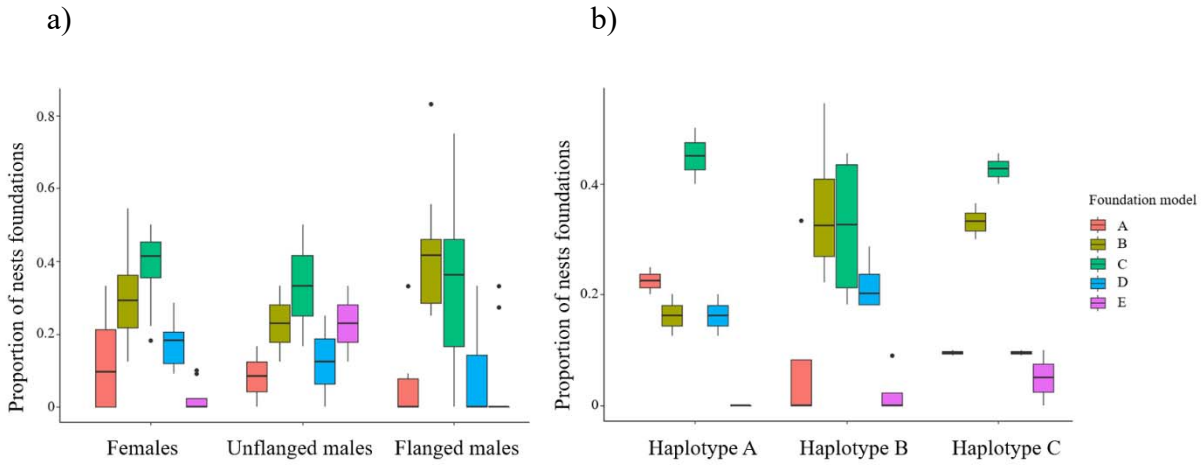
Nest architecture based on deconstructed nests

Foundation

The individuals of the Tuanan population used all five foundation models (see fig 1 in methods). The foundation types chosen most commonly by both sexes (fig. 7a) were these providing two or three existing branches as a support for the nest platform: model B (38%) and

model C (36%). Only unflanged males built more nests (21%) without foundation (model E) than any of the other classes, but the overall difference was not significant ($F(2,16)=3$, $p=0.078$). The same overall pattern was found for the different female haplotypes (fig. 7b).

Fig.7 Proportion of foundation models built by each individual, grouped by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on deconstructed nests (N=164).



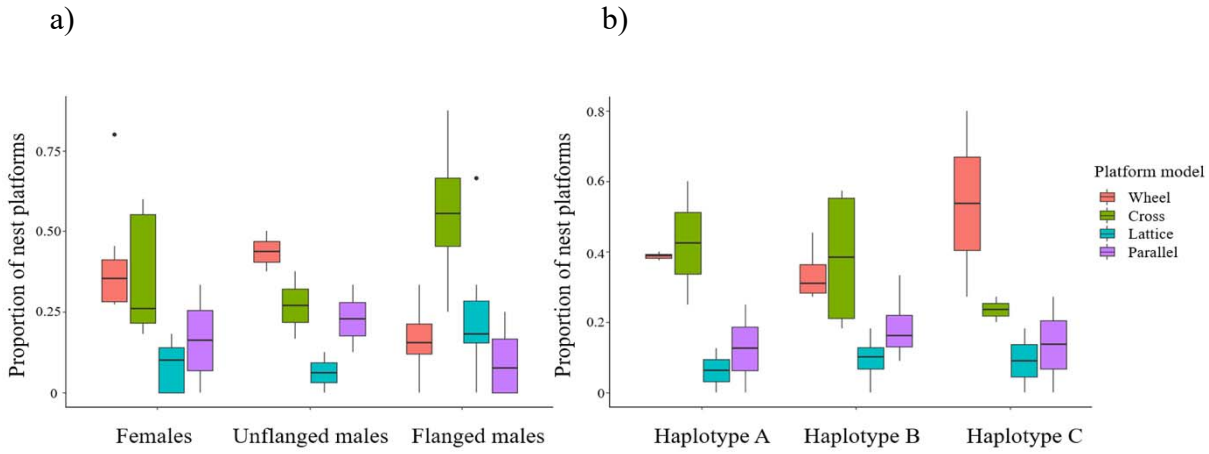
Nests without a foundation were rare among females and only females from haplotype A did not build such nests, but this result was also not significant ($F(2,5)=0.56$, $p=0.6$). At the individual level, all 18 orangutans built at least some of their nests on foundation B and C. In fact, three males exclusively used these two types. Although there was individual variation in the proportion of foundation models used, only 2 individuals, one male and one female, used the foundations B and C in less than 50% of their nests. More than half of the orangutans (N=10), for which we deconstructed a minimum of 5 nests, built them on at least 4 different foundation types (fig. s10).

Platform

Four different platform models (see fig 1 in methods) were recorded in the Tuanan population. As with the foundation, there were two models, wheel and cross, which were used in the majority of the nests by both male morphs and females (fig. 8a). There was significant variation in the frequency of building the wheel platform ($F(2,15)=6.19$, $p=0.011$). A Tukey post-hoc test showed that females built this platform model significantly more than flanged males did (adjusted $p=0.015$). However, since flanged males are much bigger and heavier that

females this might be an effect of body size. Visual inspection of the same comparison for female haplotypes (fig. 8b) did not reveal any differences. At the individual level we found much variability. More than half of the individuals (N=11) built all four platform models and all built wheel and cross platforms. Only one male did not build a wheel platform in nine deconstructed nests (fig. s11).

Fig.8 Proportions of platform models built by each individual, grouped by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on deconstructed nests (N=164).



Rim

A rim was part of the nest construction in the majority of nests (70%). There was no significant difference between females and males ($F(2,16)=0.17$, $P=0.84$; fig. 9a). Similarly, there was no significant difference among female haplotypes ($F(2,5)=0.44$, $p=0.67$; fig. 9b). Almost all individuals built nests with and without a rim (fig. s12) except for one female who built a rim in each nest sampled (N=7).

Pillow

Four pillow models were recorded in the Tuanan population. However, foot pillows were very rare and found only in 7 nests built by 6 different individuals. Here, we only focus on the 'head pillows'. The classic model of the pillow was most common, found in 50% of nests built by females and both male morphs (fig. 10a) and there were no significant differences in construction of this pillow model ($F(2,16)=1.13$, $p=0.35$). Among females this pattern predominated in haplotype A and B, while females of haplotype C used radial pillows more

(fig. 10b). There were no significant differences between female haplotypes in construction of classic ($F(2,5)=1.27$, $p=0.36$) and radial ($F(2,5)=0.83$, $p=0.49$) pillows. The majority of individuals (N=13) built all three pillow types, and all individuals (N=18) used the classic pillow. Nonetheless, the proportion of the pillow models used varied among individuals, with one female exclusively using the classic pillow in five nests that were deconstructed (fig. s13).

Fig.9 Proportion of nests with rim built by each individual, grouped by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on deconstructed nests (N=164).

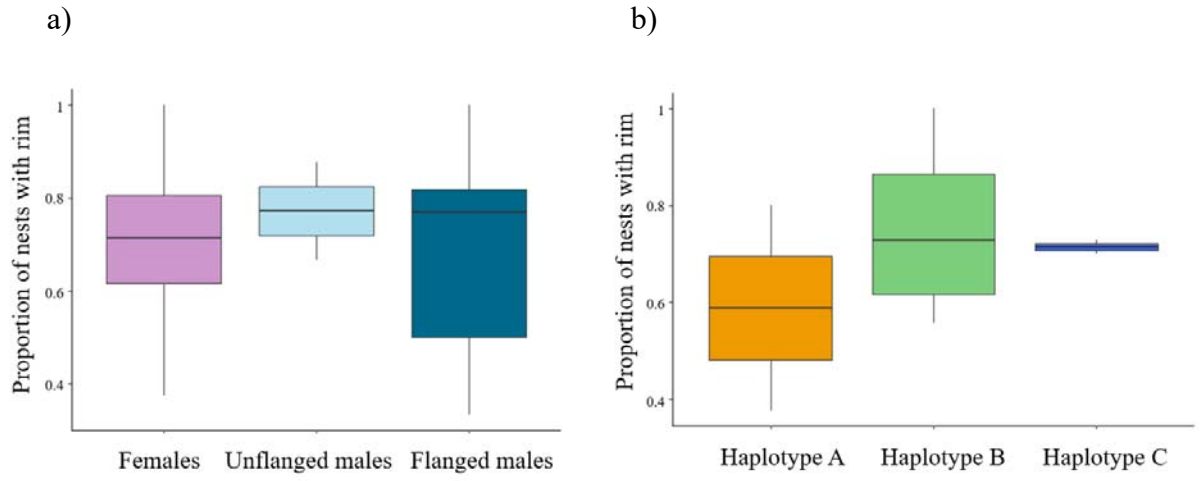
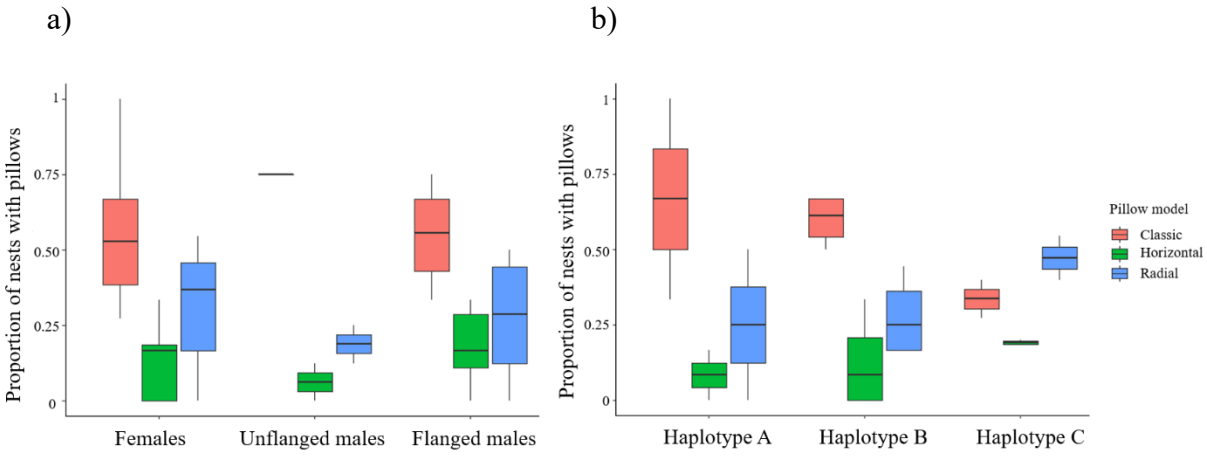


Fig.10 Proportion of pillow models built by each individual, grouped by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on deconstructed nests with pillow present (N=135).

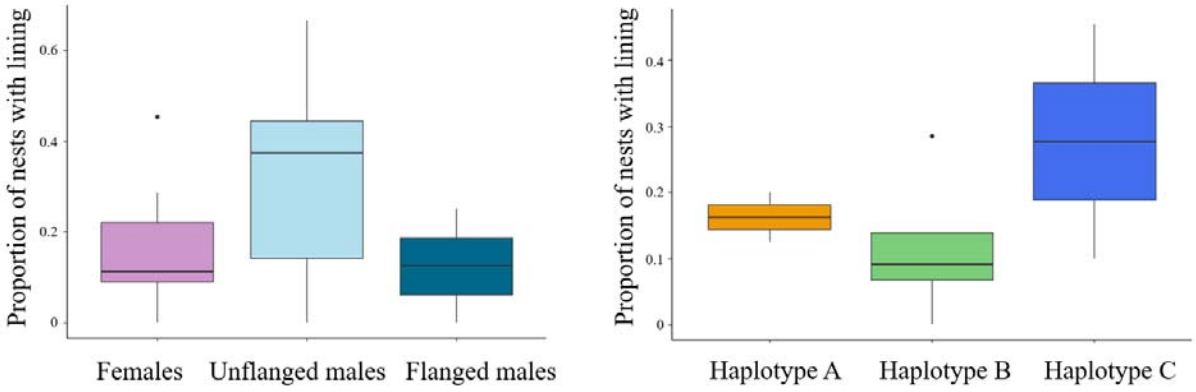


Lining

Loose branches used as additional lining inside the nest were recorded in 24% of all deconstructed nests (N=164). There was no significant difference between females and males ($F(2,16)=2.03$, $p=0.16$; fig. 11a). Also, there was no significant difference among the female haplotypes ($F(2,5)=0.79$, $p=0.5$; fig. 11b). Only two individuals, one female (Juni, N=9) and one flanged male (Teju, N=6), did not use lining in their nests (fig. s14).

Fig.11 Proportion of nests with lining built by each individual, grouped by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on deconstructed nests (N=164).

a) b)



Nest complexity

Most nests had a unique combination of different element models, each of which was built at least once by a single individual. In total, we found 109 types of nest structures (combinations of elements) in the deconstructed nests (N=164), of which only three were recorded multiple times and built by different individuals of both sexes. This results shows that all individuals can build all types of nests, and flexibly combine different models of each element as they see fit: there is not pattern in which different element models are combined in nests.

Thus we further examined nest construction by taking into account just presence or absence of different nest elements. A platform was the only element that occurred in all nests, making it the necessary element of every nest. Only 1 nest out of 164 consisted of a platform only, making it the simplest nest structure. Any additional element added to platform increased the nest complexity, with the most complex structure consisting of all elements (foundation +

platform + rim + lining + pillow + blanket). Overall, 3 types of nest structures accounted for 61% of all nest, and these included 3, 2 and 4 additional elements. The most common one (37%) consisted of 3 elements in addition to platform: foundation+rim+pillow and were built by every individual. The other two structures were both built in 12% of cases, and consisted of 2 (foundation+pillow) or 4 elements (foundation+rim+lining+pillow) in addition to the platform. Numerous individuals of both sexes and females of all haplotypes built these nests (fig. s15).

Cultural variants

Among already identified cultural variants for the Tuanan population are leaf carrying, nest smack vocalizations emitted by individuals while building the nest as well as twig biting and smoothing ends of twigs with the mouth. Below we present results on their occurrence using the data collected during focal follows.

Leaf carrying

In Tuanan, leaf carrying for nest building purposes is very rare and occurred in only 2% of all nesting events. It is a conspicuous behavior and therefore easy to observe (scored as unknown only in 4% of observed nests). Only one third of the focal individuals with ≥10 nests recorded (19 out of 57 orangutans) were observed to carry leaves. In total, 11 identified species were carried to the nests although most of them only once and by a single individual. Only leaves of *Campnosperma coriaceum* were carried repeatedly by 13 different individuals, and we therefore further investigated these instances. There was no significant difference in the occurrence of leaf carrying of this species between females and male morphs ($F(2,54)=0.81$, $p=0.45$; see also table s9, fig. 12a) nor among the different female haplotypes ($F(4,12)=0.4$, $p=0.8$; fig. 12b).

There was more variation at the individual level. Repeated leaf carrying was observed for 4 out of 7 females and 2 out of 9 males, whereas all the other individuals did it only once (fig. s16). Leaf carrying was not limited to particular locations, as it was recorded throughout the study area. Moreover, the one female (Sumi) who carried leaves into 33% of her nests did so in the area of range overlap with females of other haplotypes suggesting that non-leaf carriers had the opportunity to do so as well (fig. s17). In addition, the occurrence of leaf carrying was not explained by weather conditions such as rain (GLMM, $\beta= 0.30$, $z= 1.29$, $p=0.198$) temperature (GLMM, $\beta= 0.03$, $z= 0.14$, $p=0.801$) or fruit availability (GLMM, $\beta= 0.05$, $z= -$

0.16, p=0.874, table s9). Leaf carrying, even though rare, was observed in many females of haplotype B, none of haplotype C and just one of haplotype A. Interestingly, in all but one of the mother-daughter dyads with sufficient sample size, leaf carrying was absent or present in both (fig. 13). However, it has to be noted that the sample size for many of these females are low (<50 nests/individual).

Fig.12 Proportion of nests for which leaves were carried, grouped by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on data collected during focal follow (N=3603).

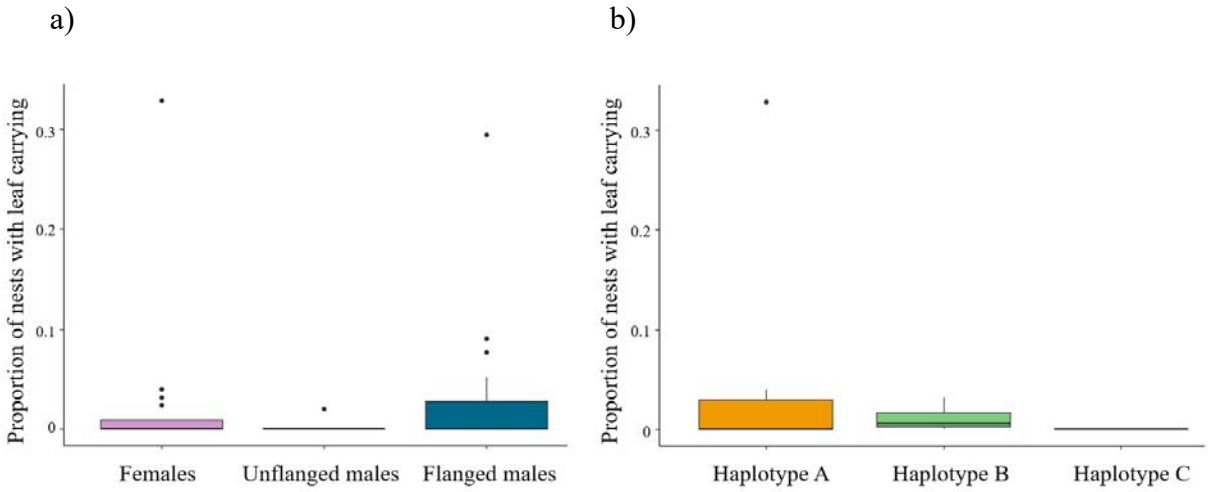
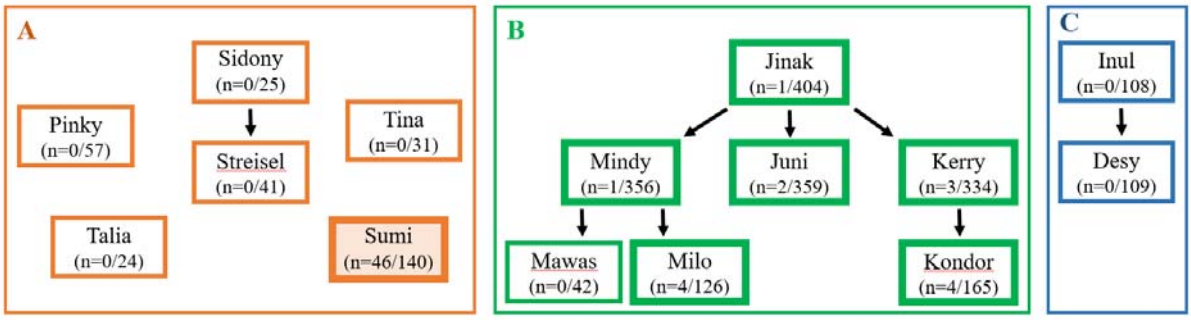


Fig.13 Leaf carrying of *Campnosperma coriaceum* for nesting purposes among females. Thick line indicates females who were observed carrying leaves of this species and the color fill indicates female who did it at the rate of >5%. The number of leaf carry events/number of nests observed is indicated in parentheses. Black arrows indicate mother-daughter pairs.



Vocalizations, twig biting and twig end's smoothing

There were some differences between females, unflanged and flanged males in giving nest related vocalizations, the so called nest-smacks (F(2,54)=4.74, p=0.013; fig. 14a). Pairwise

comparison of means with Tukey post-hoc test showed a significant difference only between females and unflanged males (adjusted p=0.011) but not between two male morphs as well as female and flanged males (adjusted p=0.059 and p=0.554 respectively). The female haplotypes did not differ in using vocalizations while nesting (F(2,12)=3.78, p=0.053; fig. 14b). All individuals in the population were observed to give nesting vocalizations at least once.

Similarly, for the presence of twig biting a significant difference was found between females and male morphs (F(2,52)= 4.1, p=0.022; fig. 15a) and the pairwise comparison of means using Tukey post-hoc test showed that the difference was significant between male morphs (adjusted p=0.017) but not between females and unflanged males and females and flanged males (adjusted p=0.130 and p=0.708 respectively). There was no difference between female haplotypes (F(2,12)=0.83, p=0.46; fig. 15b). At the individual level all females were observed to bite twigs, and 6 males were not seen to do it. However, it is important to note that this behavior was scored as unknown due to poor visibility in 52% of the total number of nests observed.

Smoothing twig ends with mouth did not differ between female and male morphs (F(2,46)=2.66, p=0.081; fig. 16a) as well as between female haplotypes (F(2,11)=1.44, p=0.28; fig. 16b).

Fig.14 Proportion of nests for which specific 'nest smack' vocalizations were produced by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on data collected during focal follows (N=3375).

a) b)

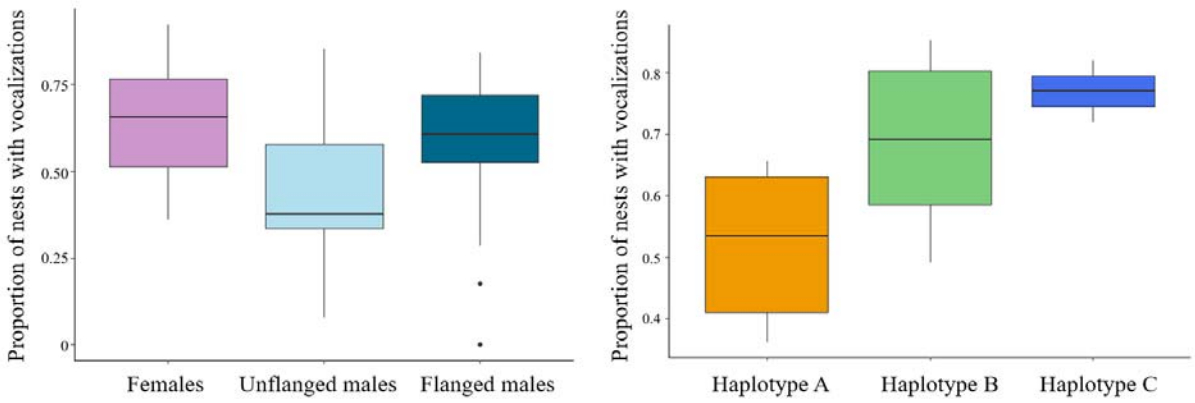


Fig.15 Proportion of nest for with twig biting, by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on data collected during focal follows (N=1782).

a) b)

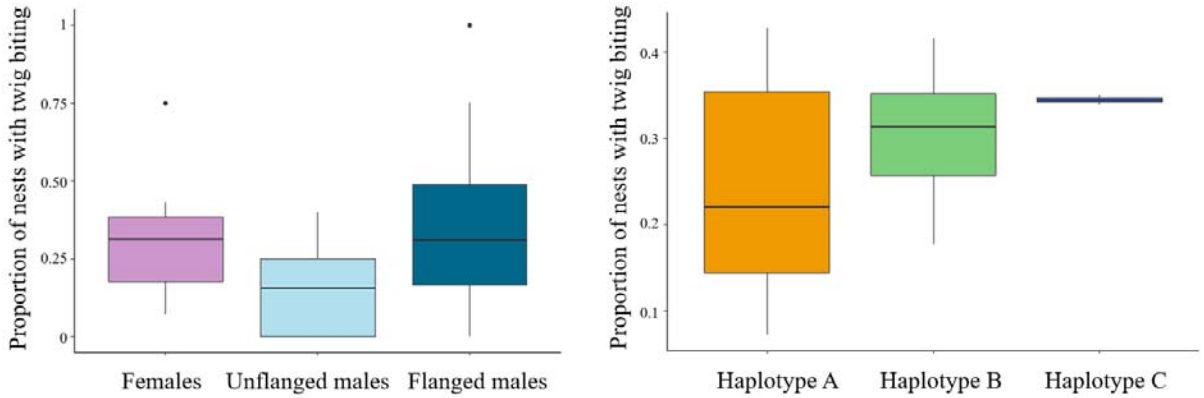
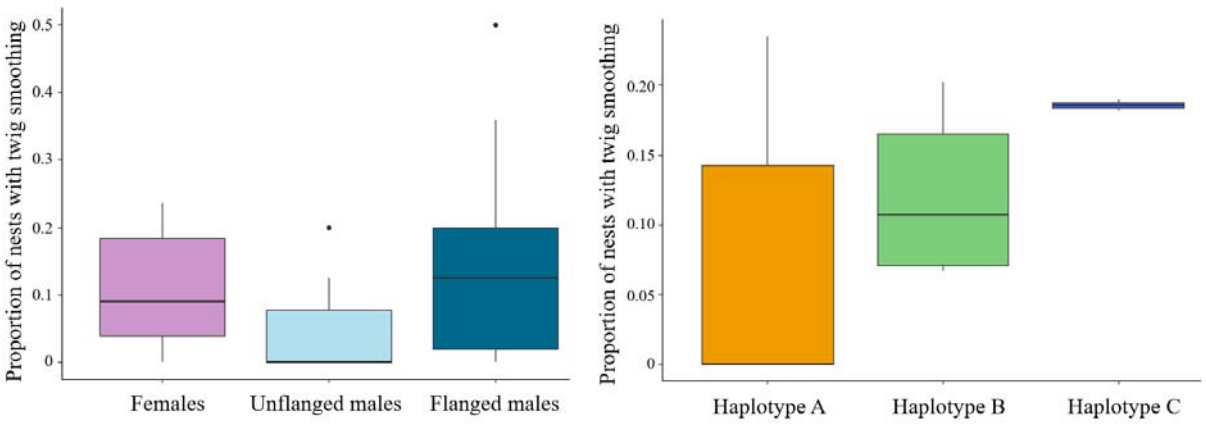


Fig.16 Proportion of nest with twig's end smoothing, by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes, based on data collected during focal follows (N=1277).

a) b)



Since all three cultural variants (vocalizations twig biting and smoothing) showed similar patterns we used Pearson's correlation to assess the relationship between them. Emitting vocalizations was positively correlated with twig biting ($r=0.43$, $p=0.001$) but not with twig smoothing ($r=0.17$, $p=0.24$). There was also a strong positive relationship between twig biting and smoothing ($r=0.62$, $p<0.001$).

Persistence of individual preference

In our long term data set we had six individuals who transitioned from unflanged into flanged male morph. This allowed us to test whether the choice of nesting tree species or nest position within a tree was consistent and reflected individual preference and knowledge or changed due to significant increase in body size. We found no differences suggesting any change in tested nest related choices between the two morphs (table s10, fig. s18). Moreover, all individuals were recorded using 'nest smack' vocalizations before and after the transition. The same was true for twig biting and twig end smoothing, although we could only consider individuals for which these behaviors were scored in ≥10 nests. It is important to note that the reliability of observing each of the behaviors differed, with vocalizations being scored as unknown on average only in 9% (±4%) while twig biting and twig end smoothing recorded as unknown in 47% (±13%) and 56% (±22%) of observed nests built by these males. As such, we have not tested statistical significance and only looked at whether the behavior occurred before and after the transition.

Discussion

Our study shows that orangutans are extremely skilled nest builders and can make use of many tree species and architecture types in which to build their sleeping platforms. The individuals have very broad nesting repertoires and show enormous flexibility in combining a variety of different element models into unique nest architectures. Yet, we also show clear preferences in both choice of nest tree and use of nest elements and their models. Many of the nesting behaviors are therefore universal for the entire population sample (i.e. the tree species, nest position choice, model of platform built, foundation used, production of nest-specific vocalizations, and twig biting and smoothing). However, others are limited to some individuals (i.e. leaf carrying of *Campnosperma coriaceum*). We therefore propose that the cultural unit may vary in size depending on behavior in question.

Tuanan orangutans built nests on almost 100 different species but only seven species were used in over half of all nests observed. This result suggests a strong preference for nest tree species choice. Preferential use of nesting materials has been found in other orangutan populations (Ancrenaz et al. 2004, Rayadin and Saitoh 2009), in chimpanzees (Hashimoto 1995, Brownlow et al. 2001, Basabose and Yamagiwa 2002, Furuichi and Hashimoto 2004, Stanford and O'Malley 2008, Samson and Hunt 2014), bonobos (Kano 1992, Fruth and Hohman

1993) and gorillas (Tutin et al. 1995, Rothman et al. 2006, Willie et al. 2014). In Tuanan, the preference for nesting tree species was the same among residents (females) and immigrants (males). However, interestingly, there are differences in the choice of nest tree species between orangutan populations inhabiting very similar habitats, i.e. peat-swamp forests located within the same region, with similar tree species composition and level of disturbance but separated and exchanging no migrants. In two sites with habitat similar to Tuanan, namely Sabangau (see Harrison et al. 2010) and Sungai Lading (see Bastian et al. 2010), orangutans used 6 tree species in half of the nests built. Only 3 in Sabangau and 2 in Sungai Lading of the most used species were the same as in Tuanan (Gibson 2005, Bastian 2008, Prasetyo et al. 2009). Particularly interesting is the difference in frequency of use of *Elaeocarpus mastersii,* a species known to have mosquito repellent properties (Florez 2007). This most commonly used tree by Tuanan orangutans was recorded only in 3% of Sabangau nests and 1% of Sungai Lading nests (Gibson 2005, Bastian 2008), despite not being rare in these areas. In fact, in Sabangau, this tree species was selected less than its availability in the habitat (Jacob's preference index D= -0.5; Gibson 2005). These differences in nest species choice between orangutan populations that are not explained by either ecological or genetic factors suggest that species choice is likely to be a local tradition, just as it is for diet, especially fallback foods (Bastian et al. 2010).

A similar conclusion can be drawn for the choice of nest position, in particular using single or multiple trees to build a sleeping platform on. In our study over half of the nests involved multiple trees (position 4) and this pattern was consistent within the population. Many orangutan populations have been observed to build multiple tree nests but with much lower frequency (less than 10% of nests). Only orangutans of two populations (Sabangau and Tuanan) showed a much higher frequency of building these nests (Prasetyo et al. 2009). Since both populations inhabit very similar forest habitats, an ecological explanation cannot be immediately excluded. However, it has been suggested that the predominance of multiple tree nests may also be cultural (Prasetyo et al. 2009). In fact, Bastian (2008) showed that building multiple tree nests was due to active choice and not to lack of suitable trees for single-tree nests. At the same time, orangutans in Sungai Lading built significantly fewer position 4 nests than orangutans in Tuanan regardless the high similarity between both sites. Since local preference for multiple tree nests were not directly due to obvious ecological factors, it is likely to be cultural.

Another, already recognized cultural variant is the nest specific vocalization. Vocalizations produced in nesting context have not only been shown to be present in some and absent in other populations but they also vary in acoustic structure between these populations

in which they are observed (van Schaik et al. 2009, Bastian et al. 2012, Wich et al. 2012). The function of these nest-related vocalizations is still unclear since they are produced equally often in the absence of association partners (pers. obs.). Moreover, because they are soft and can only be heard at a close distance they are most likely learned and spread through social transmission. It is remarkable that in Tuanan all the individuals in the population produce 'nest smacks' vocalizations in nest building context while in nearby Sungai Lading, separated by the impassable river population, these were absent (Bastian et al. 2012). However, since 89% of all nests built by Tuanan females involved 'nest smack' vocalizations, males who associated with females had a high chance to observe and learn this behavior. As such, also in case of nest vocalizations we do not distinguish a cultural unit smaller than the population.

An interesting pattern, even though the result was not significant, emerged in leaf carrying. This behavior was already described as a cultural variant (van Schaik et al. 2006, Russon et al. 2007, Bastian et al. 2012). In Tuanan, leaf carrying of particular species (*Camposperma coriaceum*) is rare and has been observed only in few individuals of both sexes. Leaves of *Camposperma coriaceum* are big, grow in bundles and in nesting context are used as pillows, lining and blankets. They increase the comfort of the nest and are known to have mosquito repellent properties (Florez 2007). As such, building nests on *Camposperma coriaceum* has its advantages but may be challenging due to the species' wood proprieties. The tree itself is rather fragile, the branches break off easily and show little elasticity compared to other tree species (pers. obs). This could explain why more than half (58%) of the nests built on this species involved additional trees. Hence, some individuals instead of using the tree for nest construction may carry its leaves to the nest.

Leaf carrying is likely to be a behavior that must be learned through direct observation and due to its rare occurrence the biggest chances of its transmission are from mother to offspring. The fact, that we observed its presence among close female relatives supports this. Moreover, knowledge about insect-repellent proprieties is a feature that is likely to be learned through personal experience (i.e. sharing nest with the mother who built nest on this tree species or carried leaves of it to the nest). This would explain why in our study haplotype B females, who are all closely related, use the species both as nesting tree as well as occasionally carry its leaves into their nests, while the C haplotype mother-daughter pair do neither. Lack of close female relatives seems to limit the spread of this behavior (see Sumi, female who had the highest rate of *Camposperma coriaceum* tree use as nesting tree and specialized in leaf carrying but had no close relatives and thus spent no time in peaceful association with the other females). Moreover, since mature orangutans rarely pay close attention to the activity of their association

partners in non-feeding contexts (Schuppli et al. 2016, Marzec et al. in prep - see chapter 4), males are also unlikely to be a vector of transmission of leaf carrying. Thus, for such rare behaviors the cultural unit is much smaller and limited to closely related female clusters (matrilines).

As mentioned above, the potential for the spread of rare, non-subsistence, comfort-related behaviors through social learning among adult orangutans who spent little time together is low. The semi-solitary lifestyle of orangutans results in a limited number of role models to learn from, as compared to group-living primates. Moreover, the fact that orangutans strongly rely on a skill set and knowledge acquired during infancy means they pay little attention to other conspecifics once they are independent, which limits the spread of new behavioral variants beyond the mother-offspring dyad. As such, nesting repertoires are not expected to easily expand in mature individuals other than through independent modifications and innovations. An immature orangutan acquires its mother's extensive nesting repertoire in full as it observes on average 2000 nests (1 nest/day for a minimum of 5.5 years) and experiences even more by sleeping in its mother's nest until the age of c.7. After that, opportunities exist, but they may not be salient enough to generate much attention.

However, direct observation and nest sharing are not the only way to acquire knowledge. Interacting with already existing nests provides an opportunity to acquire information and knowledge about nest architecture. In fact, 10% of all nests of Tuanan orangutans are reused and/or rebuilt existing ones. Moreover, information such as tree species use or nest position can be acquired simply by encountering nests built by others. Interacting or simply encountering nests allows individuals to gain information about local preference which may explain why many aspects of nest building are universal. Nonetheless, that there is something valuable to be learned may not be obvious. For instance, some of the knowledge (e.g. mosquito repellent proprieties of certain species) can only be acquired by individual experience and frequent exposure during infancy when nest sharing with mother. Hence transmission of some behaviors is limited.

These mixed conditions for spread of innovations may explain some of the mixed patterns we see. Thus, even though leaf carrying is present only in some populations, and thus presumably cultural, the poor opportunities for spreading beyond mother-infant dyads may explain why not all individuals in Tuanan carried leaves. Likewise, the fact that females of the matriline B carried leaves very rarely may suggest they had seen it done by others, but not perceiving a direct benefit obviously ascribable to its use, did not adopt the habit. Nonetheless, we may have one example of adults adopting new innovations after entering the population.

Unflanged males had lower rates of twig biting and smoothing and of nest smacking. Because flanged males did this more, this could indicate that at least some of the males coming in to the Tuanan area initially do not know about the locally specific behaviors surrounding pillow construction, but acquire this as they live there. However, within the individuals who during the study transitioned from unflanged into flanged we did not see a change in any of these behaviors. Nonetheless, all these six males were frequently seen throughout the years meaning they may have been present in the area long before the study begun. Future work could test this suggestion by focusing on recently immigrated unflanged males.

We investigated local variability in nest building behaviors of Tuanan orangutans to infer the size of the cultural unit in this species. Differences between males and females would suggest that the unit is smaller than dispersal distance, yet no such differences were found. Differences between unrelated females (i.e. female haplotypes) would suggests that the cultural unit is smaller and there is an effect of social barriers within the population that limits the spread of behavioral variants. Indeed, we found some evidence for limited transmission of some nest building behaviors, namely the use of *Camposperma coriaceum* both as a tree species to build the nest on as a well as carrying its leaves to nest. The results of our study show that most of the nest-related behaviors and choices surrounding nesting are customary among all the members of the population, while others can be limited and spread within smaller units. In conclusion, we suggest that different behaviors may spread differently within the population and therefore the size of cultural unit varies depending on behavior in question.

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Supplementary material – Chapter 2

Table s1. Results of full GLMM for stage I comparison with counts of food peering events per association per month per individual as an outcome (N=272), with wild orangutans set as the reference category, individual as random effect and ln-transformed monthly association time as an offset.

Response	Effect	Effect type	Estimate	Std. Error	z values	P-value	N (272)
Counts of food peering events/ association/ month	(Intercept)	Fixed	-5.01	0.46			
	Experienced vs. wild	Fixed	1.85	0.63	2.914	**0.004**	2
	Novice vs. wild	Fixed	3.04	0.53	5.711	**<0.001**	2
	FAI scaled	Fixed	0.079	0.22	0.351	0.726	cont.
	Log (time in association)	Offset	-	-	-	-	cont.
	Individual	Random	-	-	-	-	18
$\chi^2_{(2,5)} = 19.66$, $p<0.001$)							

Table s2. Results of full GLMM for stage II comparison with counts of food peering events per association per month per individual as an outcome (N=78), individual as random effect and ln-transformed monthly association time as an offset.

Response	Effect	Effect type	Estimate	Std. Error	z values	P-value	N(78)
Count of food peering events/ association	(Intercept)	-	-3.07	0.75			-
	Experience (novice)	Fixed	1.26	0.48	2.647	**0.008**	2
	FAI	Fixed	-0.38	0.53	-0.725	0.469	cont.
	Rehabilitation (partial)	Fixed	0.65	0.41	1.579	0.114	2
	Log (total time in association)	Offset	-	-	-	-	cont.
	Individual	Random	-	-	-	-	8
$\chi^2_{(2,5)} = 6.01$, $p=0.111$)							

Table s3. Results of full GLMM for stage I comparison with individual monthly counts of food-oriented exploratory behaviors as an outcome (N=153), with wild orangutans set as the reference category, individual as random effect and ln-transformed monthly observation time as an offset.

Response	Effect	Effect type	Estimate	Std-Error	z values	P-value	N (153)
Count of food exploratory behaviors/ month	(Intercept)	Fixed	-5.39	0.43			
	Experienced vs. wild	Fixed	1.59	0.61	2.595	**0.009**	2
	Novice vs. wild	Fixed	2.62	0.55	4.728	**<0.001**	2
	FAI scaled	Fixed	0.05	0.09	0.590	0.555	cont.
	Log (follow time a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-	-	-	19
$\chi^2_{(2,5)} = 18.08$, $p<0.001$							

Table s4. Results of full GLMM for stage II comparison with individual monthly counts of food-oriented exploratory behaviors as an outcome (N=72), with individual as random effect and ln-transformed monthly observation time as an offset.

Response	Effect	Effect type	Estimate	Std-Error	z value	P-value	N(72)
Count of food exploratory behaviors/ month	(Intercept)	-	-3.67	0.45			-
	Experience (novice)	Fixed	0.98	0.40	2.252	**0.012**	2
	FAI	Fixed	0.13	0.16	0.867	0.386	cont.
	Rehabilitation (Partial)	Fixed	-0.32	0.38	-0.835	0.404	2
	Individual	Random	-	-	-	-	9
$\chi^2_{(2,5)}$ = 6.47, p=0.091							

Table s5. Results of full GLMM for stage I comparison with minutes spent feeding on different items per month as an outcome, with wild orangutans set as the reference category, individual as random effect and ln-transformed monthly feeding time as an offset.

Response	Effect	Effect type	Estimate	Std-Error	z value	P-value	N
Minutes feeding fruit/ month (N=247)	(Intercept)	Fixed	3.69	0.04			-
	Experienced vs. wild	Fixed	-0.46	0.08	-5.88	**<0.001**	2
	Novice vs. wild	Fixed	-0.89	0.07	-12.14	**<0.001**	2
	FAI scaled	Fixed	0.04	0.00	16.75	**<0.001**	cont.
	Log (feeding hours a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-		-	19
	$\chi^2_{(2,5)}$=320.58, p<0.001						
Minutes feeding bark/ month (N=134)	(Intercept)	Fixed	0.77	0.13			-
	Experienced vs. wild	Fixed	1.75	0.24	7.392	**<0.001**	2
	Novice vs. wild	Fixed	1.79	0.22	8.160	**<0.001**	2
	FAI scaled	Fixed	0.07	0.01	9.435	**<0.001**	cont.
	Log (feeding hours a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-	-	-	19
	$\chi^2_{(2,5)}$=120.74, p<0.001						
Minutes feeding pith/ month (N=175)	(Intercept)	Fixed	0.18	0.15			-
	Experienced vs. wild	Fixed	2.30	0.28	8.133	**<0.001**	2
	Novice vs. wild	Fixed	2.40	0.26	9.172	**<0.001**	2
	FAI scaled	Fixed	-0.06	0.01	-7.566	**<0.001**	cont.
	Log (feeding hours a month)	Offset	-	-		-	cont.
	Individual	Random	-	-		-	19
	$\chi^2_{(2,5)}$=94.598, p<0.001						

Table s6. Results of full GLMM for stage I comparison with minutes spent feeding on different items per month as an outcome, individual as random effect and logged monthly feeding time as an offset.

Response	Effect	Effect type	Estimate	Std-Error	z value	P-value	N
Minutes feeding fruits/ month (N=66)	(Intercept)	-	3.11	0.09			
	Experience (novice)	Fixed	-0.36	0.08	-4.378	**<0.001**	2
	FAI	Fixed	-0.10	0.01	-8.734	**<0.001**	cont.
	Rehabilitation (Partial)	Fixed	0.29	0.09	3.380	**<0.001**	2
	Log (feeding hours a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-	-	-	9
	$\chi^2_{(2,5)}$=92,15, p<0.001						
Minutes feeding bark/ month (N=61)	(Intercept)	-	**1.92**	**0.22**			-
	Experience (novice)	Fixed	0.12	0.20	0.600	0.548	2
	FAI	Fixed	0.14	0.01	10.965	**<0.001**	cont.
	Rehabilitation (Partial)	Fixed	0.58	0.21	2.708	**0.007**	2
	Log (feeding time a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-		-	9
	$\chi^2_{(2,5)}$=122,98, p<0.001						
Minutes feeding pith/ month (N=66)	(Intercept)	-	3.15	0.14			-
	Experience (novice)	Fixed	-0.06	0.13	-0.124	0.901	2
	FAI	Fixed	-0.08	0.01	-5.837	**<0.001**	cont.
	Rehabilitation (Partial)	Fixed	-0.78	0.13	-5.842	**<0.001**	2
	Log (feeding time a month)	Offset	-	-	-	-	cont.
	Individual	Random	-	-		-	9
	$\chi^2_{(2,5)}$=49, p<0.001						

Table s7. Results of full GLMM for stage I comparison with count of item-species combinations fed per day as an outcome, with individual as random effect and ln-transformed monthly feeding time as an offset.

Response	Effect	Effect type	Estimate	Std. Error	z value	P-value	N (1251)
Count of item species combination/ day	(Intercept)	Fixed	0.58	0.03			-
	Experienced vs. wild	Fixed	0.06	0.06	0.950	0.342	2
	Novice vs. wild	Fixed	0.30	0.06	5.210	**<0.001**	2
	FAI scaled	Fixed	0.02	0.01	2.22	**0.026**	cont.
	Log (time feeding/day)	Offset	-	-		-	cont.
	Individual	Random	-	-		-	19
$\chi^2_{(2,5)}$=21.55, p<0.001							

Table s8. Results of full GLMM for stage II comparison with count of item-species combinations fed per day as an outcome, individual as random effect and logged daily feeding time as an offset.

Response	Effect	Effect type	Estimate	Std. Error	z value	P-value	N (262)
Count of item species combination/ day	(Intercept)	-	0.61	0.09			-
	Experience (Novice)	Fixed	0.27	0.08	3.474	**<0.001**	2
	FAI	Fixed	-0.05	0.03	-1.639	0.101	cont.
	Rehabilitation (partial)	Fixed	0.12	0.08	1.451	0.147	2
	Log (time feeding/day)	Offset	-	-		-	cont.
	Individual	Random	-	-		-	9
$\chi^2_{(2,5)}$=10.95, p=0.012							

Fig.s1 Minutes spent feeding on different items per feeding hour by Jambi in comparison to novice and experienced reintroduced orangutans

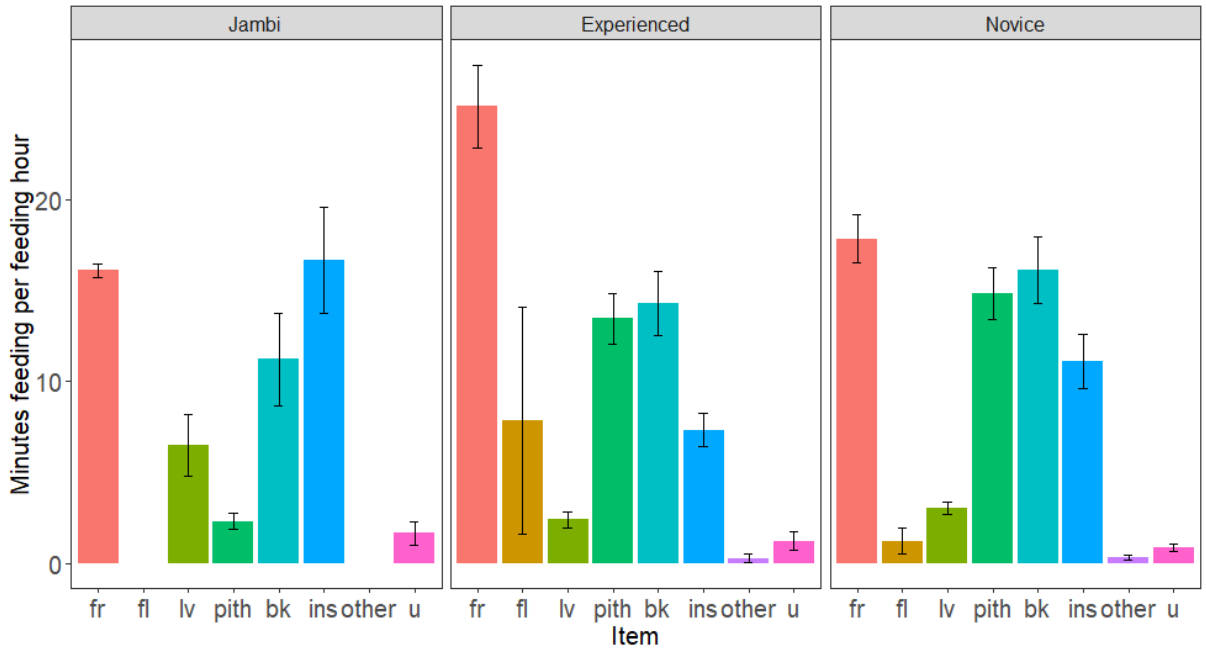


Table s9. Focal females observed in both sites Batikap and Tuanan. Table includes information about their age, class i.e. presence or absence of dependent immature as well as overview of data collected for each individual.

Individual	Site	Age	Class	Hours observed	Hours in association	N of peering events	N of food peering	N of exploratory behaviors	N of food explorations	N of recorded item-species in diet	Calculated max predicted diet	
											V_{max}	Half-time (K) needed for V_{max}
Monic	Batikap	11[a]	Mother	170.6	51.4	5	5	4	4	115	266	190
Emen	Batikap	21[a]	Mother	235.4	65.7	1	1	12	3	111	136.4	67.9
Gadis	Batikap	19[a]	Mother	248.4	32.6	1	1	10	8	232	645	411
Cindy	Batikap	22[a]	Mother	238.2	1.1	0	0	15	7	162	368	269
Compost	Batikap	15[a]	non-mother	232.6	117.5	15	9	25	18	236	268.2	56.5
Sumeh	Batikap	20[a]	Mother	245.8	0	0	0	8	6	227	300.3	90.9
Jambi (†)	Batikap	19[a]	Mother	117.3	24.6	0	0	1	0	93	114.8	42.2
Gina	Batikap	15[a]	non-mother	266.5	48.6	10	10	56	35	207	347	149
Suta	Batikap	13[a]	non-mother	220.9	19.6	1	1	8	6	318	434	93
Sofi	Batikap	14[a]	non-mother	163.3	68.8	19	17	6	5	193	484	204
Milo	Tuanan	12[b]	non-mother	898.9[c]/ 263.1[d]	141.9	2	1	22	8	150	180	225
Kondor	Tuanan	15[b]	non-mother	472.3[c]/ 191.5[d]	129	3	3	11	5	164	166.6	57.4
Juni	Tuanan	22[b]	Mother	1284.8[c]/ 296.6[d]	126.8	1	1	0	0	186	222	259
Mindy	Tuanan	30[b]	Mother	1079.8[c]/ 363.1[d]	95.1	1	0	4	1	165	166.6	92.1
Kerry	Tuanan	38[b]	Mother	920.3[c]/ 182.8[d]	99.5	0	0	0	0	123	128.7	99.1
Jinak	Tuanan	53[b]	Mother	821[c]/ 242.7[d]	10.9	0	0	0	0	119	125.3	84.2
Desy	Tuanan	24[b]	Mother	480.3[c]/ 216.7[d]	39.2	0	0	2	1	69	111	188
Inul	Tuanan	39[b]	Mother	583.5[c]/ 227.6[d]	24.4	0	0	0	0	81	94.8	151.3
Sidony	Tuanan	38[b]	Mother	332.3[c]/ 159.9[d]	5.1	0	0	1	1	93	108.7	89.5
Pinky	Tuanan	28[b]	Mother	153.6[c]/ 184.5[d]	117.4	1	1	0	0	59	55.8	14.3

(a) (†) died in 08.2016, in the middle of the study, excluded from the analysis; [a] estimated age based on teeth eruption; [b] mean of estimated age, based on number of known offspring and length of birth intervals, over the data collection period 2010-2015; [c] general dataset used for analysis of activity budget, diet composition and diet size, restricted to observation starting from 9 AM, minimum of 3 h per day and 12 h per month; [d] dataset used for the analysis of rare behaviors, restricted to data collected by selected observers and with minimum 3h per day.

Table s10. Background information of reintroduced individuals and the rehabilitation and experience categories assigned based on the age at arrival and time spent in rehabilitation, time spent with humans at young age as well as time since release.

Individual	Estimated age at arrival in rehabilitation	Estimated age at release	Months (years) in rehabilitation	Months (years) with extensive human contact/care	Rehabilitation category	Months / (years) since release	Experience category	Additional information
Monic	4	7	41 (3.4)	0	Partial	49 (4.1)	Experienced	Caged the entire time while in rehabilitation, no forest school and pre-release island
Emen	4	17	153 (12.7)	39 (+24) / 3.2 (+2)	Full	42 (3.5)	Experienced	Kept as pet for 2 years prior arrival to rehabilitation
Gadis	3	15.5	150 (12.5)	18 (1.5)	Partial	42 (3.5)	Experienced	Attended forest school and been on pre-release island
Cindy	6	19.5	162 (13.5)	0	Partial	30 (2.5)	Experienced	Did not attend forest school
Compost	2	13.3	137 (11.4)	39 (3.2)	Full	14 (1.2)	Novice	Attended forest school and been on pre-release island
Sumeh	4	19	180 (15)	14 (1.2)	Partial	9 (0.7)	Novice	Attended forest school and been on pre-release island
Jambi (†)	2	18	195 (16.2)	33 (2.7)	Full	9 (0.7)	Novice	Attended forest school and been on pre-release island
Gina	1	15	172 (14.3)	98 (8.2)	Full	0 (0.7)	Novice	Attended forest school and been on pre-release island
Suta	3.5	12.5	110 (9.2)	0	Partial	0 (0.7)	Novice	Did not attend forest school
Sofi	4.5	13.5	113 (9.4)	0	Partial	0	Novice	Caged the entire time while in rehabilitation, no forest school and pre-release island

(†) died in 08.2016, in the middle of the study, excluded from the analysis

Supplementary material – Chapter 3

Existance of social barriers within orangutan population – The dark side of the red ape: Male-mediated lethal female competition in Bornean orangutans

Table A. Compilation of observational data and video recordings collected by multiple observers on different focal individuals involved in aggressive encounter. Orangutan names were shortened to two letter codes: adult female Sidony (SI) and her offspring Sony (SO), young female Kondor (KO), unflanged male Ekko (EK) and flanged male Guapo (GU).

start time *1*	end time *2*	Observation *3*	type of attack *4*	injuries *5*	duration *6*
05:11		KO and EK depart from their nests after a copulation (too dark to see details), 2 observers with them as during a normal focal follow			
		START OF THE ASSOCIATION WITH ADULT FEMALE AND HER OFFSPRING			
13:53		Association KO & EK with SI & SO starts: observers hear noise of orangutan moving within 50m			
13:54	13:56	EK leaves KO and moves towards the noise.			
13:57		EK comes back to KO.			
13:58		EK approaches KO <2m.			
13:59		KO moves away from EK and towards the noise, EK follows KO.			
14:01		KO approaches the association member - adult female with infant (SI and SO)			
14:02		SI and KO <10m apart.	absent	absent	-
14:03		EK approaches KO and 'sexually inspects' her (sniffs her vulva)			
14:04		EK tries to copulate with KO, KO moves away.			
14:05		KO moves towards resting SI; EK follows KO, EK starts to mate with KO; SI within 5m.			
14:08		EK leaves KO and approaches SI, EK lifts SI's leg and sexually investigates, KO watches.			
14:09		KO moves towards EK and EK comes back to her, EK starts to copulate with KO again, she does not resist but still watches SI; SI also watches KO, they are <5m apart.			

1	2	3	4	5	6
14:10	14:13	KO and EK copulate; SI moves away, KO stops the copulation and leaves EK, moves towards SI; SI moves away from KO and rests but still watches her, KO approaches Si again, EK follows KO.	absent	absent	-
START OF ATTACK NO 1					
14:14	14:19	KO chases SI, SI flees, EK joins the chase; KO and EK approach and grab Si, EK pulls her down, SI falls to the ground; EK attacks Si on the ground bites her, EK leaves SI and climbs up again, Si moves away on the ground while KO comes down and approaches her, KO bites SI many times holding her, they wrestle, KO hits SI in the head SI screams, EK comes and watches them from <1m but does not join. Note SO is clinging to SI all the time, but is not attacked by either KO or EK.			
14:20	14:22	KO still fights with SI on the ground, KO bites SI in the head, SI tries to protect herself but does not fight back, SI lies on her back and is being strangled and pulled by KO, SI tries to escape, pulls her body up but KO brings her down to the ground; they stop for a moment and separate, KO moves away first, then SI climbs up, but EK gets in her way and attacks, now EK hits SI, she runs to the ground and tries to escape, KO and EK chase after her, EK grabs SI first and starts biting her leg and hand, KO watches.	continuous and coordinated; initiator: KO; attack: KO, EK	severe	12min
14:22	14:25	KO and EK do not let SI run away, when EK attacks SI KO watches and stays in SI's way preventing her escape, EK and KO take turns, when EK stops physical aggression KO approaches and bites SI again while EK watches and guards the victim.			
14:25	14:26	EK climbs up and pushes over dead tree, KO still on the ground bites and hits SI.			
END OF ATTACK NO 1					
14:27		Fight stops, KO leaves SI, SI climbs up and rests.			
START OF ATTACK NO 2					
14:28	14:36	KO approaches SI and EK follows, SI moves away climbing further up, KO follows first, but EK approaches fast and KO lets EK pass, EK gets to SI first; second attack: EK pulls SI down, SI falls to the ground, KO attacks and bites SI many times, SI does not fight back, So clings all the time, EK joins KO and hits and bites SI too, KO and EK are pushing SI, for first time both attack her at the same time, SI tries to move away but KO follows	continuous, coordinated; initiator: KO; participate: KO, EK	severe	9 min
END OF ATTACK NO 2					
14:37	14:38	SI rests with EK and KO on opposite sides.			

1	2	3	4	5	6
START OF ATTACK NO 3					
14:39	14:41	EK <2m from SI, KO <5 above her. Third attack: KO moves towards SI, EK follows and approaches SI first, grabs and shakes her, KO above them, EK lets go and SI falls; SI moves away climbs up again, tries to escape, EK approaches SI and bites her again; observers hear a noise of OU approaching within 50m, KO and EK stop the attack and SI moves away, KO and EK follow SI and maintain proximity of <5m; SI has deep wound on her right leg;			
14:42	14:43	EK approaches and grabs SI again, bites her while holding; KO joins, SI falls to the ground, EK stays above while KO bites SI, SO clings and cries, SI screams; SI moves away on the ground and climbs up, tries to leave, EK follows her KO also approaches; observers again hear noise of other OU now within 30m; KO approaches SI while EK travel towards newcomer and almost immediately comes back to SI;	continuous, coordinated, initiator: KO, attack: KO, EK	severe	7 min
14:44	14:46	EK approaches SI from below while KO is above her, EK pulls her to the ground, bites her and hits, holds her hand so she can't escape (“coercive handhold”); there is a movement <10m away and attack stops for 10 sec, all OU listen to the noise but EK still holds SI by her wrist, he pulls her down again and bites, she falls but grabs a branch before falling all the way to the ground, EK and SI wrestle but SI escapes from EK and moves away, EK follows her; the fight stops again and orangutans separate, SI moves in opposite direction from KO and EK.			
END OF ATTACK NO 3 AND ARRIVAL OF FLANGED MALE					
14:47	14:48	Flanged male (GU) arrives, GU approaches SI, SI does not move away, GU long calls and sexually inspects SI, EK and KO approach, EK shakes the tree and displays, GU leaves SI and chase after EK.	-	-	-
14:49		EK runs away, GU stops chasing him but moves slowly toward EK, who runs further away; KO approaches SI and watches her	-	-	-
14:50	14:58	GU comes back and mates with SI, SI cooperates; KO watches from <5m, she approaches and bites SI's hands while GU still copulates with SI, GU seems to protect SI, moves around blocking KO's access to SI, SO clings during whole episode.	-	-	-
14:59		EK approaches GU and SI, GU interrupts mating leaves SI and approaches EK , while KO approaches SI and reaches in her direction but is too far to grab her, KO moves closer; SI vocalizes and GU looks into KO's direction; KO stops.	unsucessfull attempt	-	-

1	2	3	4	5	6
15:00	15:04	GU comes back to SI, KO above <3m and EK <10m, KO moves towards SI and GU, GU long calls, SI vocalizes when KO approaches <1m, SI stays close to GU.	-	-	-
15:05	15:09	SI and GU copulate again, KO watches and comes closer, KO pulls SI's arm twice: fist time shortly 5 sec and second time she holds it for about 35 sec, then KO sniffs and licks her fingers, she looks at SI's wound; KO bites SI's hand shortly (5 sec), SI screams, KO moves back, GU long calls, KO moves closer again, SO throws himself at KO and tries to bite, KO moves back, GU moves away from SI, copulation finished, GU looks up, SI screams and moves towards him, GU waits and moves with SI (coordinated travel in contact) away from KO.	three single and short attacks, KO	by KO: bite wound on the hand	45 sec
15:10	15:13	GU moves away and KO immediately approaches SI, GU come back to SI, KO stops, this repeats several times each time GU prevent KO from touching SI, just by being next to her.	several unsucessful attemts	-	-
15:14		SI rests, GU above her but they are in contact, KO above GU	-	-	-
15:15	15:17	SI moves away from KO together with GU (coordinated travel), SI rests, GU moves away >5m	-	-	-
15:18	15:19	KO approaches SI, SI kiss-squeaks and GU approaches SI fast, KO tries to bite, GU approaches KO, but KO does not move away, KO just sniffs and touches SI (no more biting)	unsucessfull attempt	-	-
15:20	15:24	GU between KO and SI, SI moves away and kiss squeaks, GU follows her and stays above.	-	-	-
15:25	15:26	GU approaches SI and KO, GU and SI are almost touching, both rest, KO >2m	-	-	-
15:27		Suddenly KO bites SI twice, SI screams, GU displays, shakes branches, KO moves away a 2m, SI approaches GU to contact	single and short, just KO	by KO: bite wound on the hand	10 sec
15:28		GU moves away 5m, KO tries to bite SI's leg, SI screams, GU comes back and KO stops	single and short, just KO	no injuries	5 sec
15:29	15:32	KO bites her again, SI screams, SO hits KO in the head also pushes her head away while she tries to bite SI's hand, KO sniffs SI's genitals, tries to touch SO and then bites SI's foot; SO hits KO in the head again; SI screams GU approaches and KO moves 3 m away	twice single and short, just KO; one unsuccessful attempt	by KO: bite wound on the foot	10 sec
15:33		KO tries to bite SI, SO hits KO 3 times	unsuccessful attempt	no injuries	-

1	2	3	4	5	6
15:34		GU still above SI, GU moves 3m away from SI, immediately KO approaches SI, GU watches KO	-	-	-
15:36	15:37	KO attacks SI again, GU displays shaking the tree, he is 3m away from SI and KO, KO immediately stops and moves > 5 m away from SI.	single, just KO	no injuries	10 sec
15:38		SI rests.			-
15:39	15:40	GU approaches SI, KO moves away, GU does not chase KO and is not aggressive towards her, but his presence keeps her away from SI, EK still within <50m. GU displays when EK approaches to <20m.			
15:41	15:47	GU moves toward EK but when KO approaches SI, GU returns to SI right away, GU stays near SI.			
15:48	15:54	GU rests between SI and KO.			
15:55		KO tries to grab SI, SO slaps KO.	absent	absent	-
15:56		GU displays shakes tree next to SI, then rests.			
16:00		All seems quiet, KO feeds on liana, SI moves away slowly, EK still < 20m feeds on liana too.			
16:01		GU moves towards EK but only 6m away from SI, EK now just 10m away from GU.			
16:05		GU climbs towards KO, KO moves higher up.			
16:14		GU passes above SI, KO stays at distance.			
16:19	16:36	SI rests, SO sucks and grooms SI's wounds, drinks the blood dripping from deep wound in her arm, he clings all the time and sucks all her major wounds, KO < 5m away watches SI & So.			
16:36	16:42	SO again cleans wound on SI's leg and drinks the blood, SI moves away from KO, KO does not follow her, GU still close, EK >10 m away but still in association, SI moves away from GU but stays within 10 m distance.			
16:43		GU approaches SI <5m.			
16:44		SI starts feeding, SO sucks blood from SI’s wounds	absent	absent	-
16:45	16:50	SI builds a night nest, KO and GU still feed, EK still <50m away.			
16:52		KO builds her night nests 30m away from SI.			
17:08		GU longcalls towards EK who is <50m away.			
17:22	17:27	GU builds night nest halfway between SI and KO; EK makes nest last at 20-50m from each of the others			

Supplementary material – Chapter 4

Within-population variation in nest building behaviors of Bornean orangutans (*Pongo pygmaeus wurmbii*): individual plasticity and cultural influences

Table s1. Number of tree and ground nests as well as events of night sleep on the ground without building a nest by mature individuals of known sex in Tuanan, between 2003 and 2018. Note that only flanged males slept on the ground without building a nest and all the female ground nests were built by one individual.

	Female	**Male**
Tree nests	4031	2256
Ground nests	5	19
Overnight sleep on the ground without nest	0	116
Total	4036	2391

Table s2. Number of arboreal night and day nests built, rebuilt and reused by mature individuals of known sex in Tuanan between 2003 and 2018.

		Female	**Male**
Night nests	New	2787	1659
	Rebuilt	282	146
	Reused	9	12
Day nests	New	785	396
	Rebuilt	97	18
	Reused	71	25
Total		4031	2256

Fig.s1 Tree architecture types, modified from Halle and Oldeman (1970).

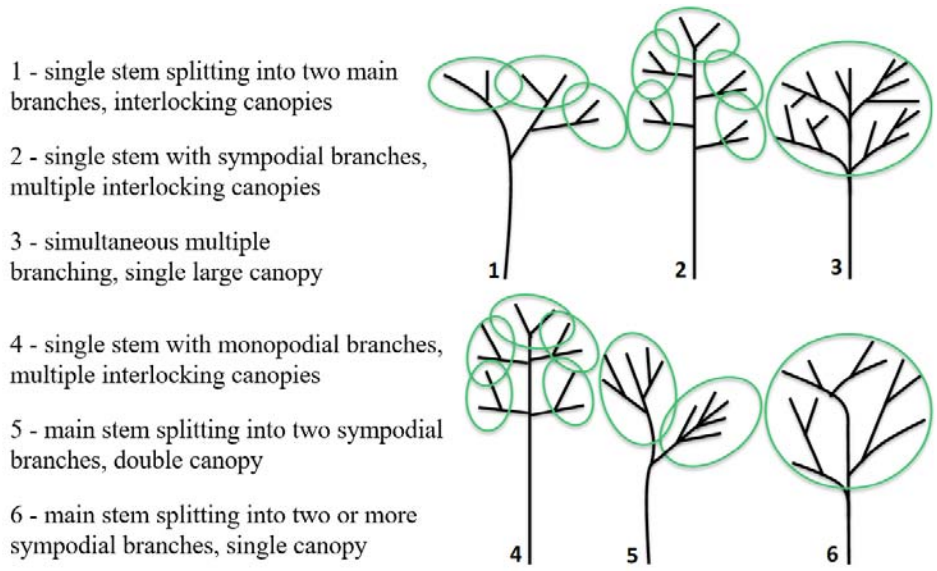
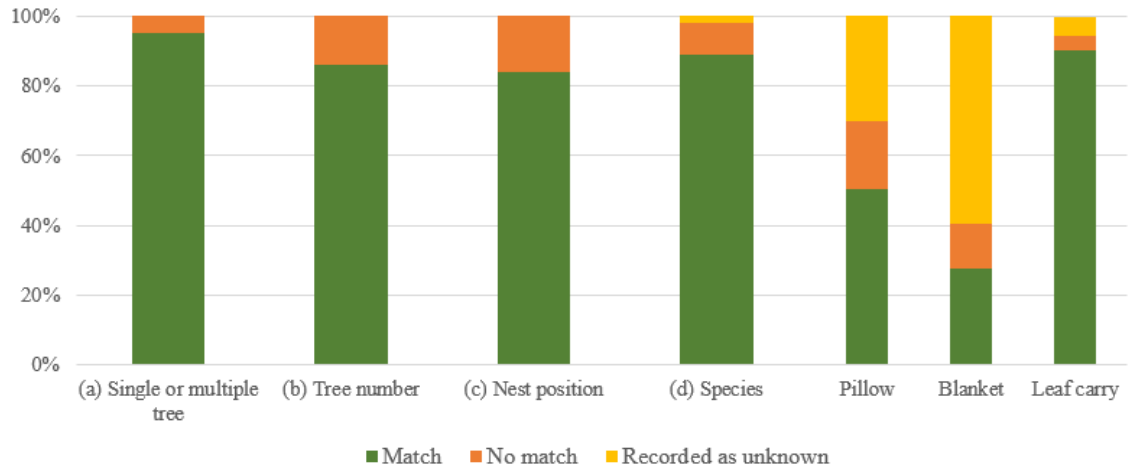


Table s3. Cohen's Kappa (K) reliability scores for four categories of nest data collected during focal follows (N=200) based on data acquired during nest deconstruction.

Category	p_o	p_e	**K**
Single or multiple tree nest (N=200)	0.95	0.52	0.90
Number of trees (N=200)	0.86	0.004	0.859
Nest position (N=200)	0.84	0.42	0.73
Species of main nest tree (N=200)	0.89	0.05	0.83
Pillow (N=131)	0.73	0.70	0.08
Blanket (N=76)	0.96	0.72	0.86
Leaf carry (N=178)	0.98	0.93	0.66

$K = \frac{p_o - p_e}{1 - p_e}$ where: p_o – is a relative observed agreement between datasets, and
p_e – is a hypothetical probability of chance agreement

Fig.s2 Reliability of nest data (N=200) collected during focal follows compared to data from deconstructed nests.



(b) The nests were correctly scored as either single or multiple tree nests in 95% of the follow data.
(c) The number of trees involved in the nest recorded during the follow matched the deconstructed data in 86%. In fact, in the majority of cases (24 out of 28) the number was lower than the actual number of trees involved (i.e. higher in data set of deconstructed nests than scored during focal follows). It was more common to mistakenly record multiple tree nests as being built on a single tree (N=9) than the opposite (N=2).
(d) The nest position, while still highly reliable, was recorded incorrectly during focal follows in 16% of nests.
(e) The main tree species was incorrect in 32 nests compared to the data collected during nest deconstruction. However, it is important to note that in these 32 cases observers noted the main tree as unknown on 4 occasions and in 9 cases recorded the main tree as a second tree involved in the nest.

Table s4. Sample sizes of nest data collected during focal follows between 2003 and 2018 and during nest deconstruction between 2013 and 2015: 1) the total data set, 2) the data used for assessing reliability of data collected during focal follows (the matched sample of deconstructed nest with nests observed during focal follows), and 3) the restricted data set including only night, new and arboreal nests built by mature, individually identified orangutans with minimum sample size per individuals of ≥10 and ≥5 in the behavioral and deconstructed nest datasets, respectively.

	Data from behavioral observation	Data from nest deconstruction
Total dataset	6427	200
Dataset used for IOR	200	200
Restricted dataset used for analysis	3750	164

Table s5. Sample size of both: observed nests (*ON*) and deconstructed nests (*DN*) for each class.

Sex	Class	Observed nests		Deconstructed nests		Remarks
		N of nests	N of indiv.	N of nests	N of indiv.	
Females	haplotype A	338	6	13	2	*ON*: one mother-daughter pair, rest females not closely related; *DN*: non mother-daughter
	haplotype B	1864	7	38	4	all closely related females
	haplotype C	223	2	21	2	mother-daughter
	haplotype N	13	1	-	-	excluded from analysis
	haplotype P	40	1	-	-	excluded from analysis
Males	unflanged	278	13	14	2	*ON*: 6 males developed flanges during study period thus are present in each class
	flanged	994	28	78	9	

Table s6. List of all tree species used in single-tree nests and as main tree in multiple-tree nests, built by females (F), unflanged (UFL) and flanged (FL) males. The species are ordered by the total frequency of use.

Species - main tree	**Local name**	**F**	**UFL**	**FL**	**Total**
1	*2*	*3*	*4*	*5*	*6*
Elaeocarpus mastersii	Mangkinang blawau	416	60	202	678
Litsea sp.	Tagula daun besar	211	21	119	351
Campnosperma coriaceum	Tarantang	194	19	63	276
Neoscortechinia kingii	Karandau biasa	151	20	82	253
Tetractomia tetranda	Rambangon	121	19	67	207
Koompassia malaccensis	Bengaris	96	14	47	157
Nephelium maingayi	Piais	114	14	25	153
Shorea sp.	Maranti	88	6	19	113
Mezzettia umbellata	Kambalitan	61	4	13	78
Xylopia fusca	Rahanjang bawi	57	5	15	77

1	2	3	4	5	6
Nephelium lappaceum	Rambutan hutan	61	5	11	77
Garcinia bancana	Mangis hutan daun kecil	37	4	22	63
Santiria cf. laevigata	Kayu sapat	41	3	14	58
Garcinia sp.	Mangis hutan daun besar	36	2	20	58
Syzygium sp.	Tatumbu putih	38	4	14	56
Sandoricum beccarianum	Papung	40	5	9	54
Shorea sp.1	Maranti daun kecil	32	1	17	50
Diospyros pseudomalabarica	Tutup kabali	30	3	15	48
Palaquium leiocarpum	Hangkang	33		13	46
Palaquium pseudorostratum	Nyatoh puntik	33	4	9	46
Mesua sp.	Enyak beruk	25	5	15	45
Mezzettia leptopoda	Mahawai umb	34	1	10	45
Tristaniopsis whitiana	Balawan	27	7	7	41
Litsea rufo-fusca	Kamehas daun perak	29	3	9	41
Cryptocarya sp.	Kamehas	35	1	3	39
Palaquium ridleyi	Nyatoh undus buah merah	25	2	11	38
Blumeodendron kurzii	Karandau putih	19	3	11	33
Stemonurus scorpioides	Keput bajuku	24	1	7	32
Musaendopsis beccariana	Kayu lalas	19	4	6	29
Payena leerii	Nyatoh undus daun ujung	20	2	6	28
Lithocarpus conocarpus	Pampaning	20	3	4	27
Polyalthia hypoleuca	Mahawai 2	19	1	4	24
Mezzettia umbellata	Mahawai	17	3	3	23
Calophylum sp.	Mahandingan	14	1	6	21
Palaquium sp.	Nyatoh undus	16	2	3	21
Diospyros confertiflora	Kayu tulang	11	1	6	18
Pouteria malaccensis	Lewang	9	2	7	18
Myristica lowiana	Kumpang	13	1	3	17
Syzygium garcinifolia	Tapuhut putih	13		3	16
Eugenia curtisii	Galam tikus	12		3	15
Myristica lowiana	Maruang	10	2	3	15
Palaquium cochlearifolium	Nyatoh undus buah besar	10		4	14
Gymnacranthera farquhariana	Kumpang daun hijau	9	1	3	13
Gonystylus bancanus	Ramin	7	3	2	12
Syzygium havilandii	Tatumbu kasar	7		5	12
Syzygium nigricans	Tatumbu merah	9		3	12
Gardenia leiocarpum	Hantangan	5	2	4	11
Aglaila sp.1	Kajalaki	8		2	10
Chisocheton sarawakanus	Latek manuk	4	1	5	10
Syzygium sp.1	Tatumbu pohon merah	5	1	4	10
Garcinia parvifolia	Gandis	6		3	9
Buchanania sp.	Rangas parei	5		3	8
Cotylelobium melanoxylon	Rasak	7		1	8
Licania splendens	Bintan	4		3	7
Madhuca motleyana	Katiau	4	1	2	7

1	*2*	*3*	*4*	*5*	*6*
Dactylocladus stenostachys	Martibu	4	1	2	7
Dialum sp.	Keranji	6			6
Ctenolophon parviflorus	Madang rambut merah	4	1	1	6
Cratoxylum glaucum	Mipa	5		1	6
Shorea balangeran	Kahui	5			5
Ilex cymosa	Kambasira	5			5
Ficus sp.	Lunuk	3		2	5
Xanthophyllum sp.	Kambasira hatue	1		3	4
Horsfieldia crassifolia	Kumpang daun perak	2		2	4
Litsea sp.	Madang pahawas	4			4
Shorea parvistipulata	Maranti daun besar	4			4
Platea sp.	Tambalik angin	4			4
Artocarpus dadak	Tampang	1	1	2	4
Tetramerista glabra	Tantimun	2	1	1	4
Garcinia sp.	Barania hutan	2	1		3
Xerospermum noronhianum	Damon	2		1	3
Diospyros sp.	Ehang haduk	3			3
Aglaila sp.	Kajalaki hatue	2		1	3
Pternandra coerulescens	Kambasulan	1	1	1	3
Calophyllum sclerophyllum	Kapurnaga jangkar	3			3
Ficus sp.1	Lunuk beringin	2	1		3
Diospyros siamang	Pinding pandang	2		1	3
Litsea sp 1.	Tagula daun kecil	2		1	3
Magnolia sp.	Hanyer bajai	1	1		2
Xanthophyllum ecarinatum	Kamuning	1		1	2
Cryptocarya sp.	Karamuan	2			2
Ficus sp.2	Lunuk kecil	1		1	2
Parartocarpus venenosus	Pakan	2			2
Dyera lowii	Pantung	1		1	2
Xylopia sp.	Rahanjang batu	2			2
Xylopia sp.1	Rahanjang hatue	2			2
Microcos sp.	Rewui	1	1		2
Alseodaphne sp.	Gemur		1		1
Aglaia rubiginosa	Kajalaki bawi	1			1
Ploiarium alternifolium	Kayu asam	1			1
Santiria sp.1	Kayu sanaman			1	1
Santiria sp.	Langset kalawet		1		1
Ctenolophon sp.	Madang	1			1
Antidesma cf. cuspidatum	Nonang	1			1
Sterculia sp.	Pendo			1	1
Castanopsis foxworthyii	Takurak	1			1
	Total trees	***2478***	***278***	***994***	***3750***
	Total species	***92***	***55***	***73***	***96***

Fig.s3 Jacob's preference index for tree architecture types (N=164) used by Tuanan orangutans, where 1 = indicates total avoidance; +1= indicates preferential use and 0 = proportional use.

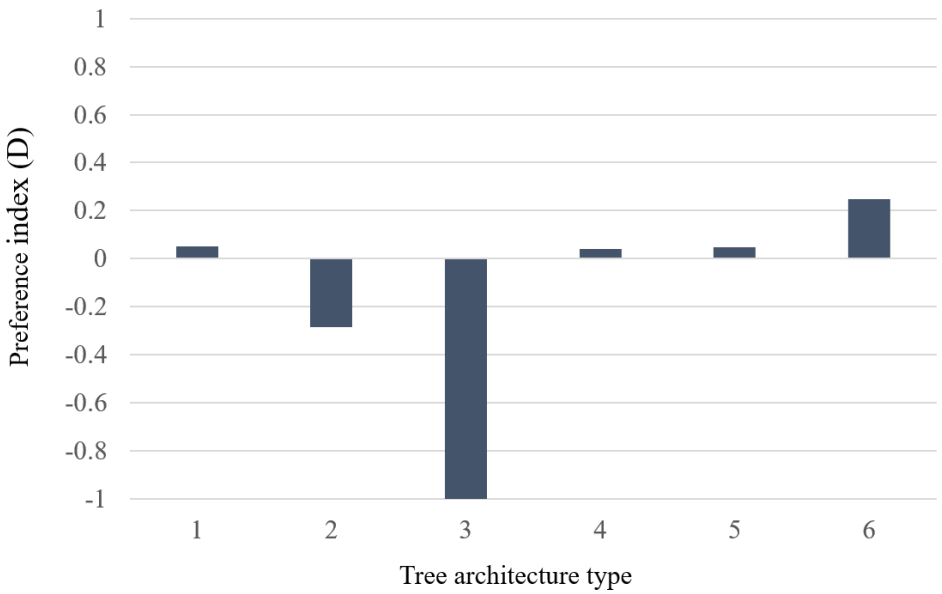


Fig.s4 Tree architecture of all the trees from the seven most used nest species recorded in the nest plots (N=476) and making up 25% of all trees (N=1939) recorded in these plots.

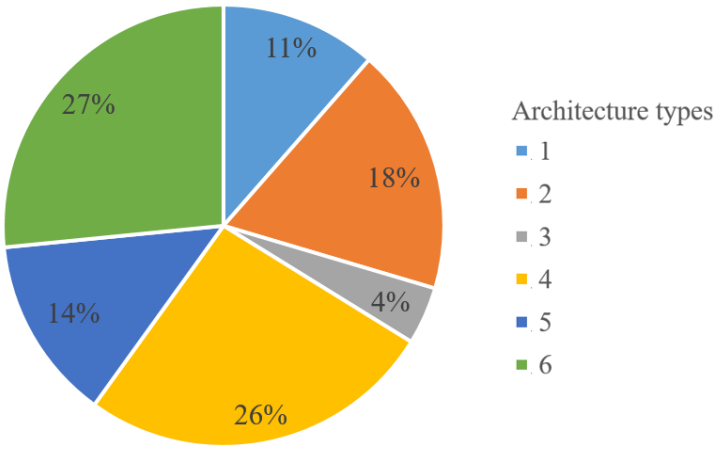


Fig.s5 Variation in tree architecture of the seven most used nesting tree species.

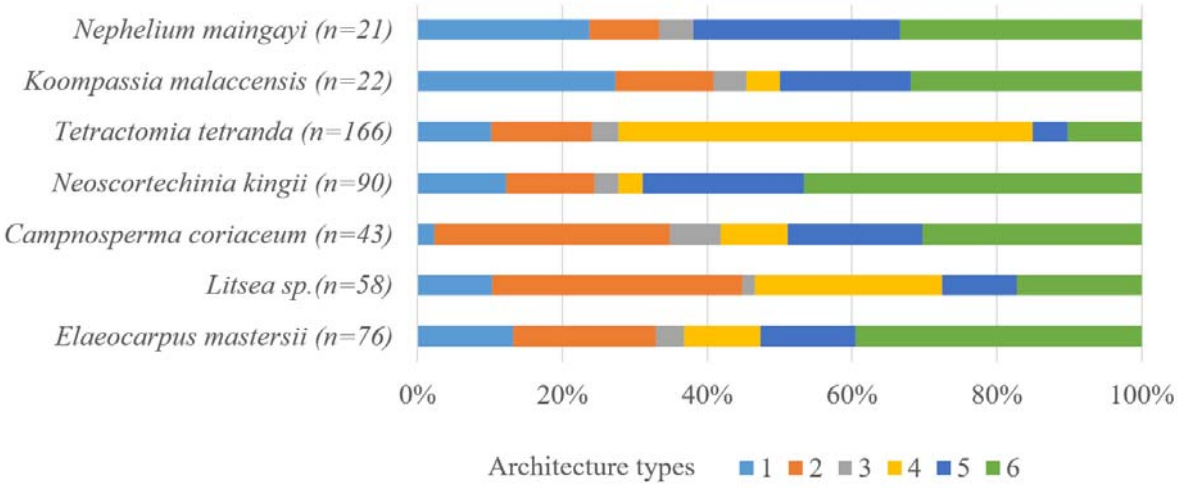


Fig.s6 Percentage of nest position built by Tuanan orangutans. The sample consists of 3750 nigh nests built by 51 mature individuals both sexes.

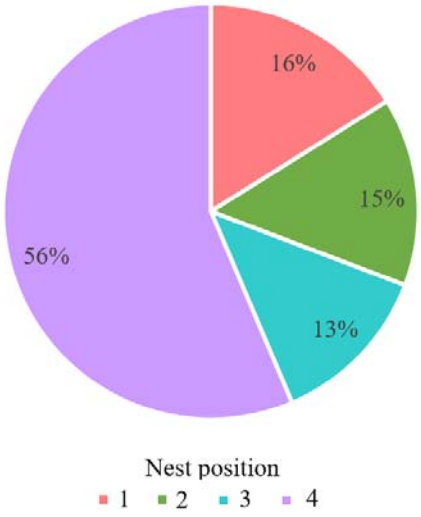


Table s7. Results of a comparison of nest positions built by different classes (females, unflanged and flanged males), using ANOVA with Bonferroni correction of α= 0.05/4 = 0.0125.

		Df	Sum sq	Mean Sq	F value	P value
Pos 1	Class	2	0.000	0.000	0.02	0.98
	Residuals	54	0.378	0.007		
Pos 2	Class	2	0.024	0.012	1.14	0.33
	Residuals	54	0.561	0.010		
Pos 3	Class	2	0.106	0.053	4.71	0.013
	Residuals	54	0.606	0.011		
Pos 4	Class	2	0.099	0.050	2.29	0.98
	Residuals	54	1.172	0.022		

Table s8. Results of a comparison of nest positions built by different female haplotypes (A, B and C), using ANOVA with Bonferroni correction of α= 0.05/4 = 0.0125.

		Df	Sum sq	Mean Sq	F value	P value
Pos 1	Class	2	0.011	0.005	2.22	0.15
	Residuals	12	0.029	0.002		
Pos 2	Class	2	0.001	0.001	0.06	0.94
	Residuals	12	0.109	0.009		
Pos 3	Class	2	0.001	0.000	0.04	0.96
	Residuals	12	0.153	0.013		
Pos 4	Class	2	0.009	0.005	0.16	0.85
	Residuals	12	0.349	0.029		

Fig.s7 Proportion of nest positions built by each individual: a) females (arranged by haplotype, N=2478), b) unflanged males (N=278) and c) flanged males (N=994).

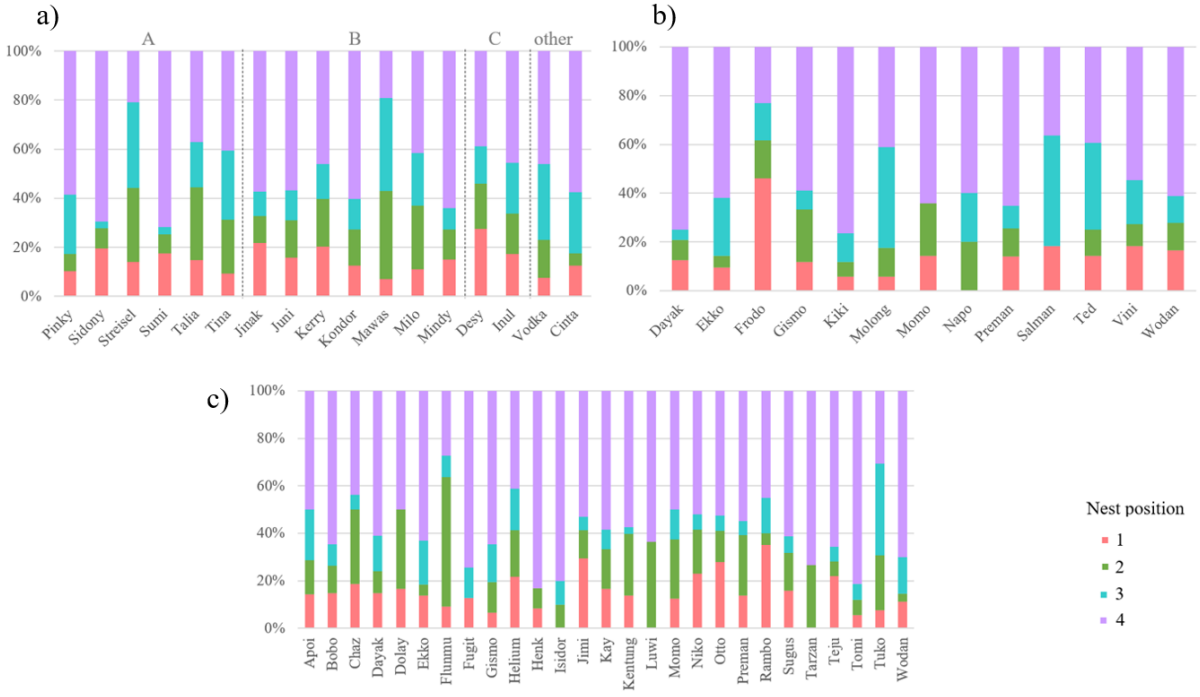


Fig.s8 Proportion of single- and multiple-tree nests built by mature individuals of Tuanan (N=3750).

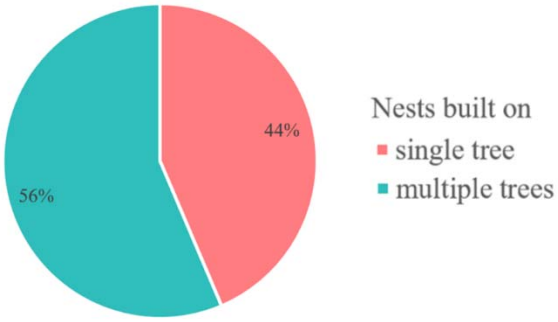


Fig.s9 Proportion of nests built on either single or multiple trees calculated per individual and grouped by a) males and females, with males divided into unflanged and flanged, and b) different female haplotypes

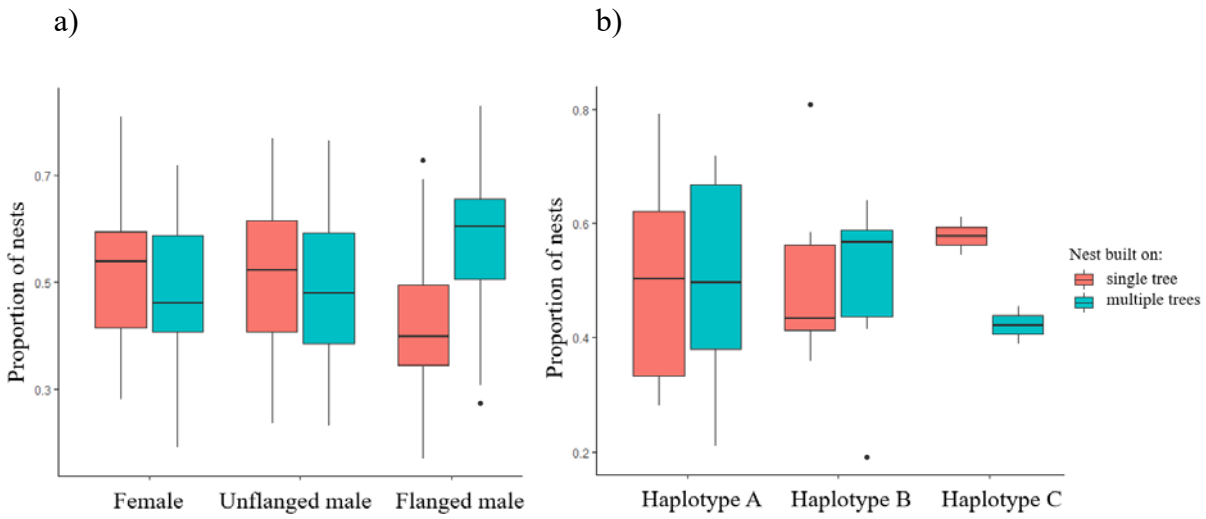


Fig.s10 Proportion of nest foundation models used by all individuals: females by haplotype, unflanged males (UFL), and flanged males (FL) based on deconstructed nests (N=164).

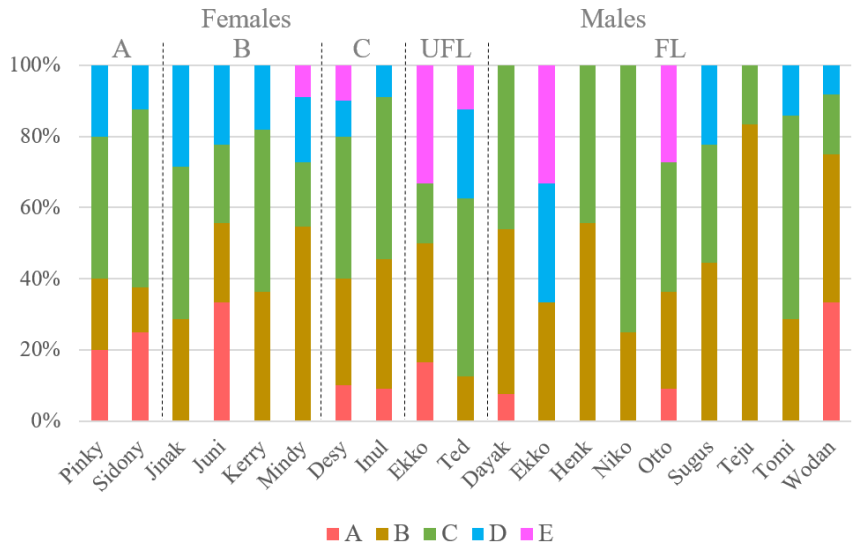


Fig.s11 Proportion of nest platform models built by all individuals: females by haplotype, unflanged males (UFL), and flanged males (FL) based on deconstructed nests (N=164).

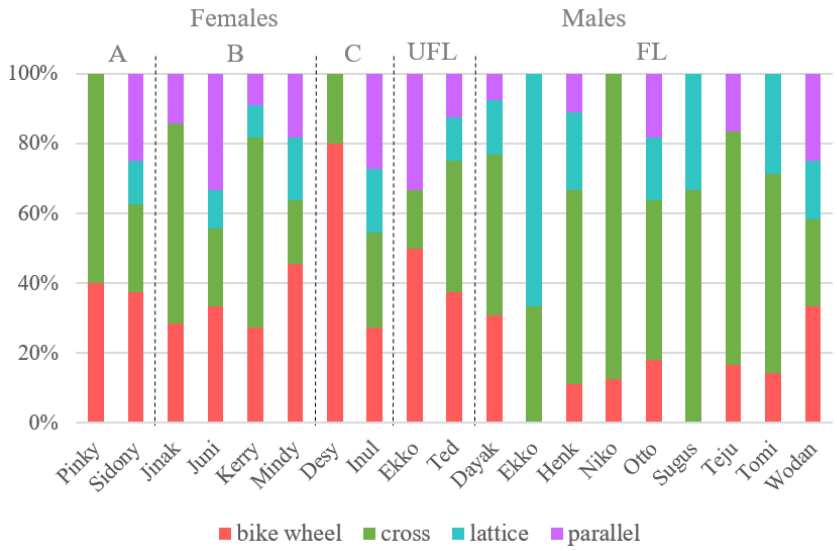


Fig.s12 Proportion of rims built as a part of the nest by all individuals: female indicating which haplotype they belong to A, B, C, unflanged males (UFL) and flanged males (FL) based on deconstructed nests (N=164).

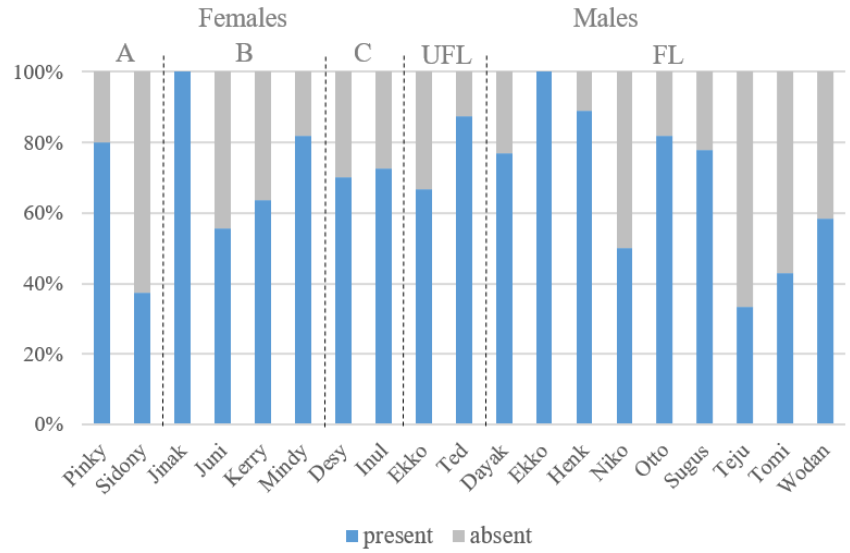


Fig.s13 Proportion of pillow models built by all individuals: female indicating which haplotype they belong to A, B, C, unflanged males (UFL) and flanged males (FL) based on deconstructed nests (N=164).

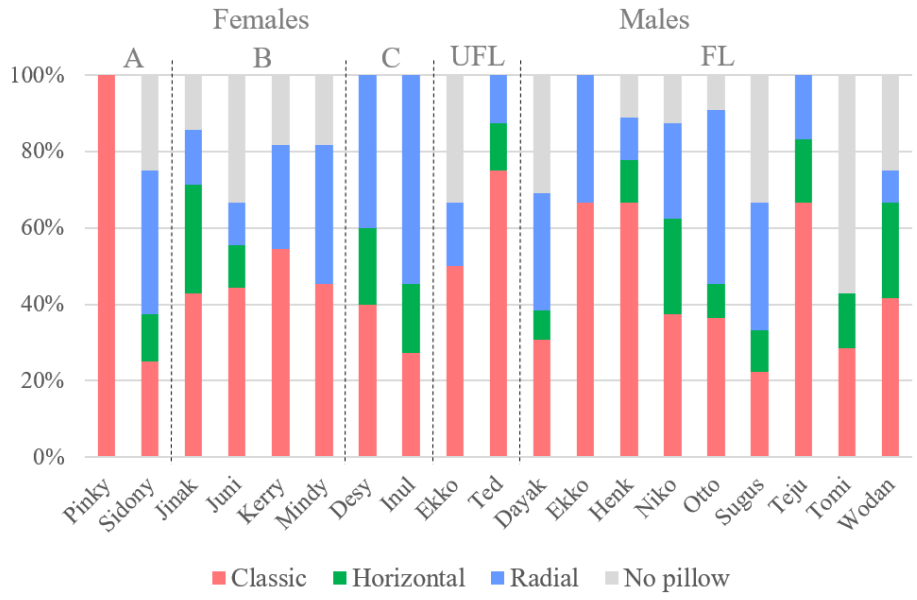


Fig.s14 Proportion of nest with lining built by all individuals: female indicating which haplotype they belong to A, B, C, unflanged males (UFL) and flanged males (FL) based on deconstructed nests (N=164).

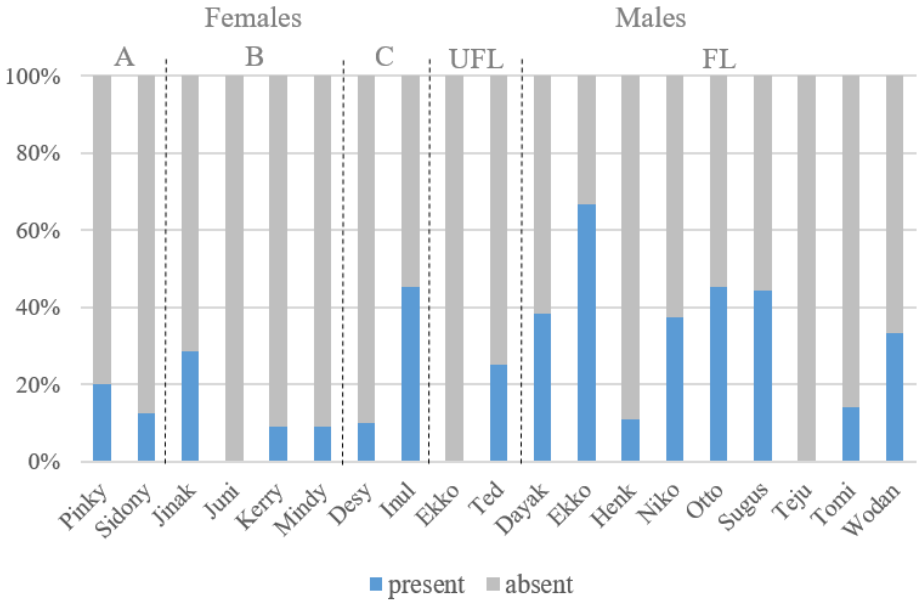


Fig.s15 Individual variation in nest architecture and complexity of the deconstructed nests built by of females from three haplotypes and males. The 18 unique nest structures with different combination of additional elements added to platform are color coded, the element names are shortened to first letter and number of letters equals number of elements built (i.e. f – foundation; r – rim; p – pillow; l – lining; b – blanket).

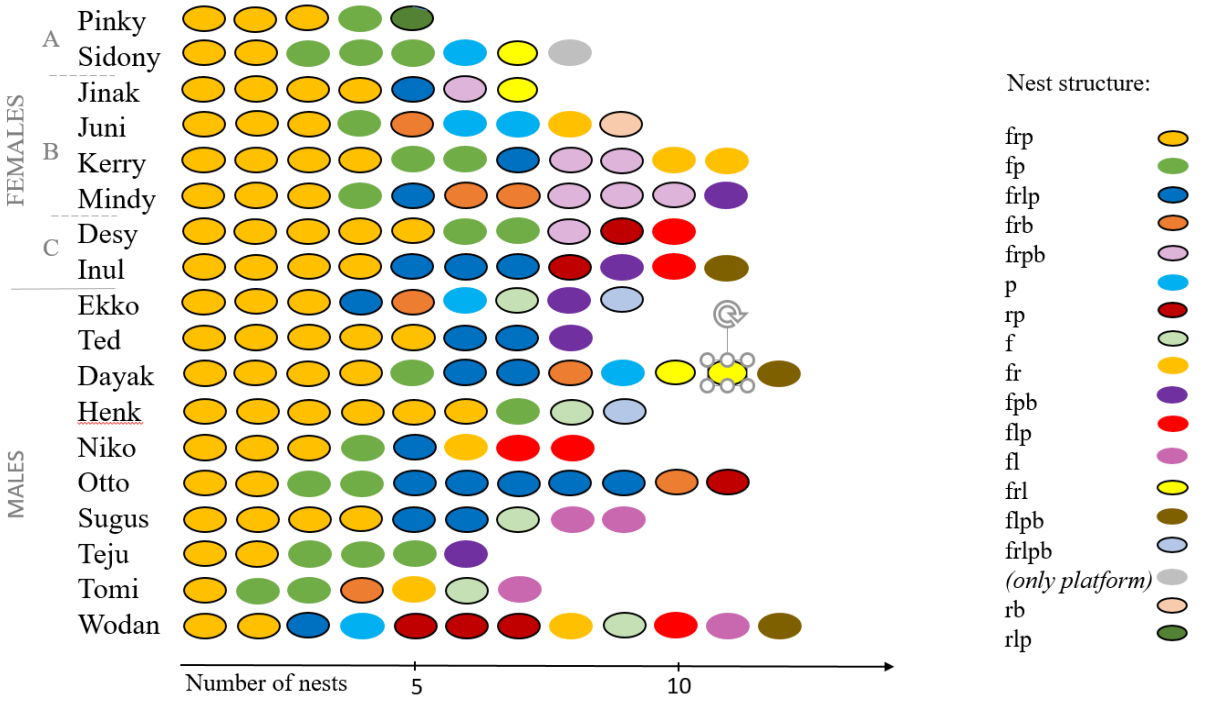


Fig.s16 Percentage of nests for which leaf carrying of *Campnosperma coriaceum* was recorded in all nests observed (N=3603). Only 16 individuals (7 females and 8 males) were observed to perform this behavior. Note, that the other 35 individuals never carried leaves to nesting site.

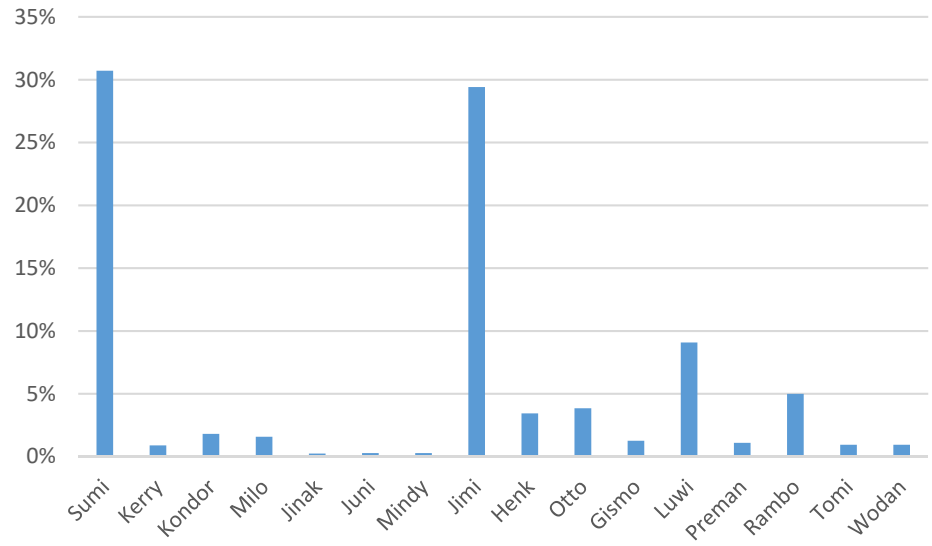


Fig.s17 A map of the Tuanan study area (grey lines represent the trail system) showing the degree of overlap between the ranges of the females of each haplotype. The polygons represent the 95% isopleth of the Kernel density estimation for the sum of all location of all females of each haplotype. The shaded area is Sumi's individual home range (95% isopleth of the Kernel density estimation). Points show location of *Camposperma coriaceum* leaf carrying observations, where black points represent leaf carrying by seven different males, green by six females of haplotype B and orange by Sumi, the only haplotype A female who was observed to carry leaves of this species.

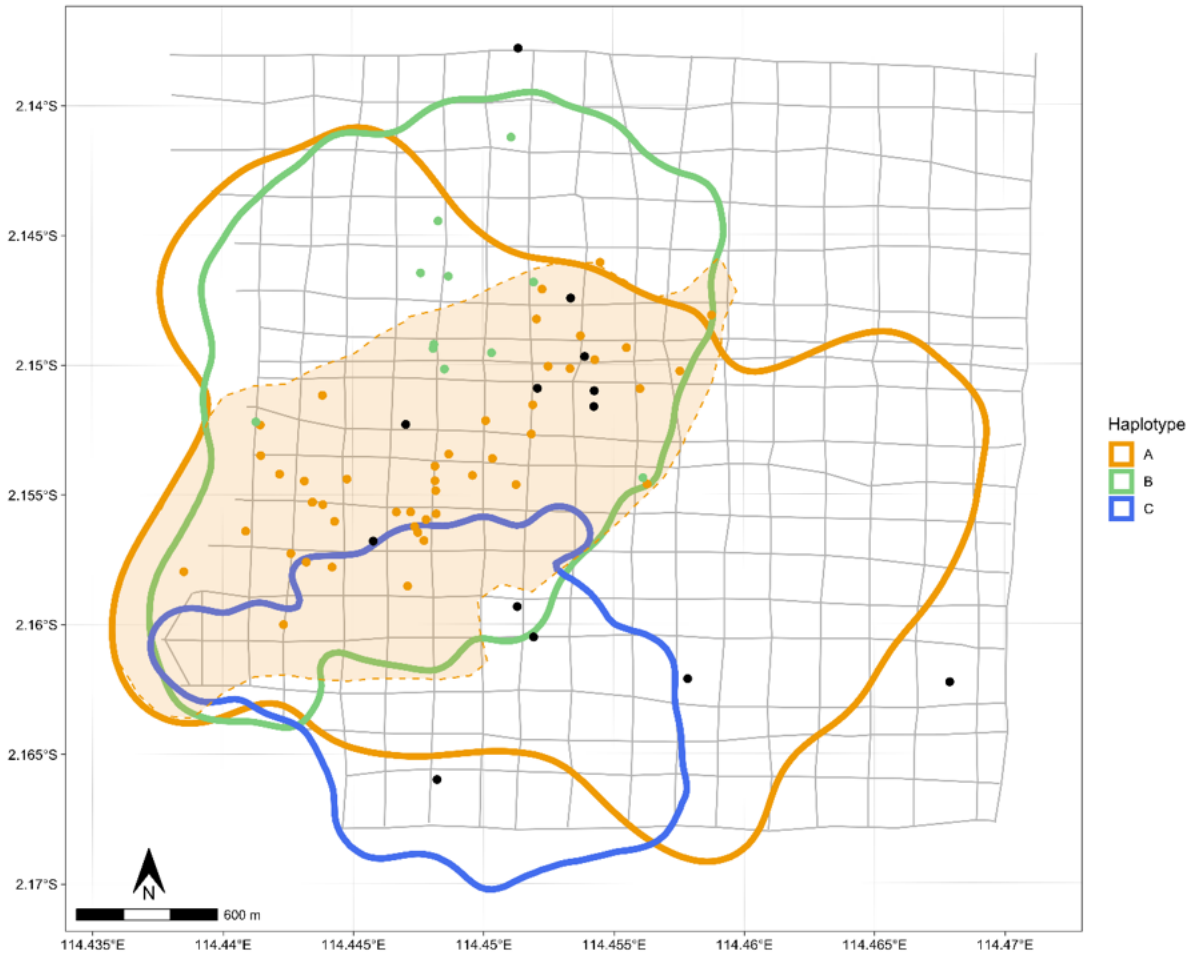


Table s9. Results of binomial GLMM with presence of leaf carrying as a response variable, fruit availability (FAI), temperature and rain as a fixed effects, sex and individuals as random effect.

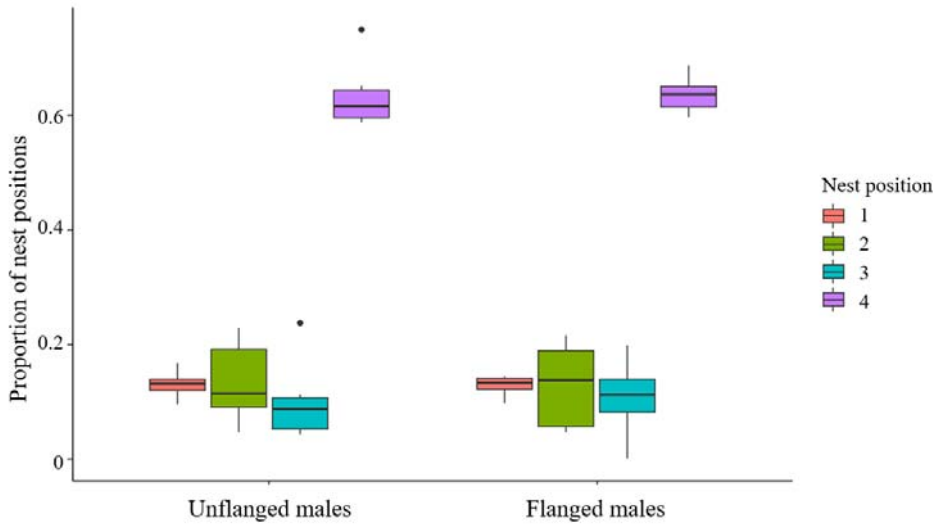
Effect	Type of effect	Estimate	Std. Error	Z value	P value	N(3441)
FAI	fixed	-0.008	0.05	-0.16	0.874	cont.
Temp	fixed	0.035	0.14	0.25	0.801	cont.
Rain (yes)	fixed	0.382	0.30	1.29	0.198	2
Sex (male)	Fixed	-0.012	0.81	-0.02	0.988	2
Individual	Random	-	-	-	-	55

Table s10. Within-individual comparison of nest position and tree species selection by males who during the study period transitioned from unflanged to flanged. P-values obtained using Fisher's exact test. The top 7 species (used in >50% on nests built by all individuals of the population) included: *Elaeocarpus mastersii, Litsea sp., Campnosperma coriaceum, Nephelium maingayi, Tetractomia tetranda, Koompassia malaccensis, Neoscortechinia kingie.*

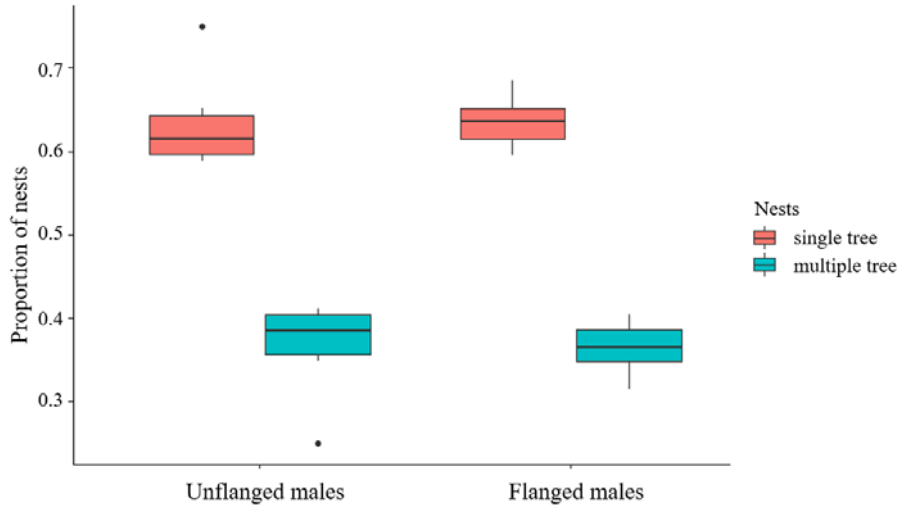
Name	Total sample size		P-value		% of nests built on 7 most used species	
	unflanged	flanged	Nest position	Tree species	unflanged	flanged
Dayak	24	54	0.574	0.3	58%	57%
Ekko	21	65	0.940	0.7	76%	60%
Gismo	51	31	0.5	0.7	63%	45%
Momo	14	8	0.799	1	64%	88%
Preman	43	51	0.390	0.2	49%	59%
Wodan	18	90	0.374	0.07	83%	60%

Fig.s18 Comparison of six males who over the study period developed from unflanged into flanged. The individual proportions were used to visualize a) nest position, b) single and multiple tree nests and c) nest tree species choice of the two male morphs.

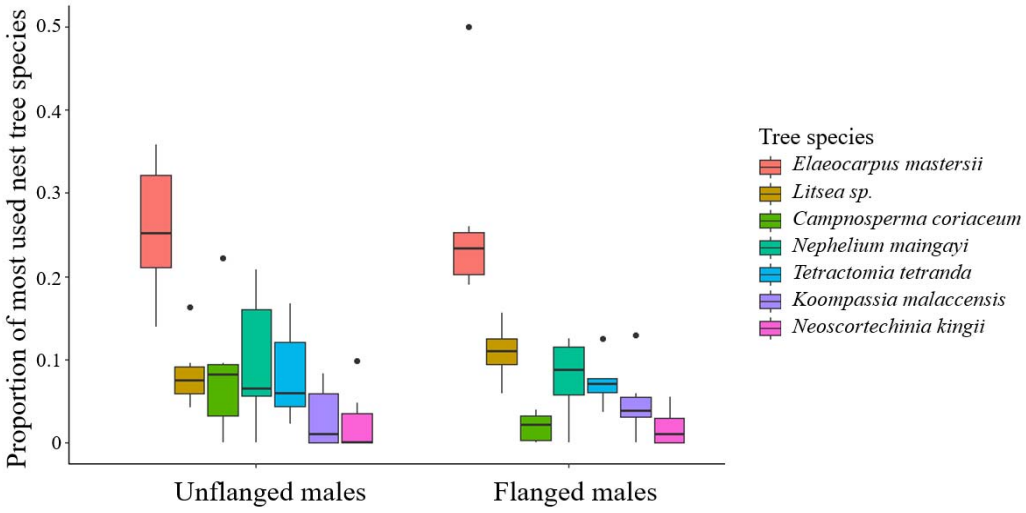
a)



b)


Proportion of nests
0.7
0.6
0.5
0.4
0.3
Unflanged males
Flanged males
Nests
single tree
multiple tree

c)


Proportion of most used nest tree species
0.5
0.4
0.3
0.2
0.1
0
Unflanged males
Flanged males
Tree species
Elaeocarpus mastersii
Litsea sp.
Campnosperma coriaceum
Nephelium maingayi
Tetractomia tetranda
Koompassia malaccensis
Neoscortechinia kingii

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